JAN 1 0 1937

JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND BY

PROFESSOR E. BARCLAY-SMITH — UNIVERSITY OF LONDON
PROFESSOR J. P. HILL — UNIVERSITY OF LONDON
PROFESSOR J. T. WILSON — UNIVERSITY OF CAMBRIDGE
PROFESSOR H. H. WOOLLARD — UNIVERSITY OF LONDON
PROFESSOR SIR ARTHUR KEITH — ROYAL COLLEGE OF SURGEONS
LINCOLN'S-INN-FIELDS, LONDON, W.C.2

VOLUME LXXI
PART I
OCTOBER 1936

Entered at New York Post Office as Second Class Matter

(All Rights reserved)

LONDON
CAMBRIDGE UNIVERSITY PRESS
FETTER LANE, E.C. 4
CHICAGO: The University of Chicago Press
(Agents for the United States)
BOMBAY, CALCUTTA, MADRAS: Macmillan
TOKYO: Maruzen Company Ltd.

All rights reserved.

Price Ten Shillings net

PRINTED IN GREAT BRITAIN

BIOMETRIKA

A Journal for the Statistical Study of Biological Problems

Volume XXVIII, Parts I and II

CONTENTS

I. An Examination of Investigations by Dr Maurice Fishberg and Professor Franz Boas dealing with Measurements of Jews in New York. By G. M. MORANT and OTTO SAMSON. II. On Jewish-Gentile Relationships. By KARL PEARSON. III. Method of Moments and Method of Maximum Likelihood. By KARL PEARSON. IV. Cleft Palate, Hare Lip, Dacryocystitis, and Cleft Hand and Feet. By E. A. COCKAYNE. With two Plates and Pedigree. V. Influence of Position on Structure of Inflorescences of *Cicuta maculata*. By WILLIAM DOWNES BATEN. With one Plate and four Figures in the Text. VI. A Biometric Study of the Human Mandible. By G. M. MORANT with the assistance of MARGOT COLLETT and N. K. ADYANTHÁYA. With three Plates and one folding Table. VII. On the Craniology of Oceania. Cranis from New Britain. By GERHARDT VON BONIN. With Map, eight Plates, three folding Tables of Measurements, six Contours in Text, and the same on tissue in pocket at end of issue. VIII. A Study of an Egyptian Series of Mandibles. With Special Reference to Mathematical Methods of Sexing. By E. S. MARTIN. With two Plates.

Miscellanea

(i) An Illustration of the Accuracy of the χ^2 Approximation. By M. R. EL SHANAWANY. (ii) Note on the Application of a Theorem of Frau Pollaczek-Geiringer. By J. PRZYBOROWSKI and H. WILENSKI. (iii) Note on the Method of Moments. By V. ROMANOVSKY. (iv) On the Validity of a Certain Pearson's Formula—a Rejoinder. By JAN WEINIEWSKI.

The Subscription price, *payable in advance*, is 45*s.* inland, 50*s.* export, per volume (including postage). Double parts 32*s.* net. Cheques should be drawn to BIOMETRIKA and sent to "The Secretary, Biometrika Office, Department of Statistics, University College, London, W.C. 1."

Issued by THE BIOMETRIKA OFFICE

University College, London

Recently Published

ILLUSTRATIONS OF REGIONAL ANATOMY

By E. B. JAMIESON, M.D., Sen. Demonstrator & Lecturer, Anatomy Department, University, Edinburgh

Complete in Five Sections

SECTION		PLATES	COLOURED	UNCOLOURED	PRICE	POST
I.	CENTRAL NERVOUS SYSTEM	48	31	17	7s. 6d.	5d.
II.	HEAD AND NECK	61	45	16	10s. 6d.	6d.
III.	ABDOMEN	37	27	10	5s. 6d.	4d.
IV.	PELVIS	30	14	16	3s. 6d.	4d.
V.	THORAX	27	20	7	4s. 6d.	4d.
	COMPLETE SET	203	137	66	30s. 0d.	7d.

Each Section is attractively bound in limp leaf covers for ready reference.

Two Further Sections to be published in October: Section VI, UPPER LIMB, 48 plates, 7s. 6d. net, postage 5d. Section VII, LOWER LIMB, 52 plates, 10s. net, postage 6d. All the Plates in these two Sections will be coloured, with the exception of three in the Upper Limb.

An illustrated prospectus can be obtained post free on application.

E. & S. LIVINGSTONE *Medical Publishers* **16 & 17 Teviot Place, Edinburgh**

medical
Faison

SIR GRAFTON ELLIOT SMITH

M.A. (CAMB.), LITT.D. (MANCH.), D.SC. (LIVERP.), M.D., CH.M. (SYDNEY)
F.R.C.P. (LOND.), F.R.S.

Awarded Croix de Chevalier de la Légion d'Honneur, May, 1936.

A BIOGRAPHICAL SKETCH OF HIS EARLIER CAREER

It is now nearly fifty years since I first became aware of Grafton Elliot Smith, then just on the threshold of the domain of biological science to which he was destined to make so substantial a contribution.

Early in 1887 I had migrated, as a teacher of anatomy, from the University of Edinburgh to the recently established Medical School of the University of Sydney. At some time during that year, I can well remember my senior colleague, Anderson Stuart, drawing my attention to a remarkable school-boy examination paper which had come under his notice in examining in the subject of Physiology in the then "Senior Public" examination—the equivalent of a "Higher" school, or "leaving", examination. This candidate proved to be a member of the gifted family of the highly respected headmaster of one of the larger "public" or State schools in Sydney.

In the following year, at the age of seventeen, young Elliot Smith entered the University of Sydney as a student of medicine. The first year of the curriculum in medicine was at that time devoted almost entirely to purely "Arts" subjects, literary and mathematical; the medical science studies only beginning in the second year. This comparative breadth of study in the curriculum in medicine had a good deal to recommend it, and its later abandonment under pressure of the increasing demands of more specialized scientific and medical subjects was a regrettable necessity.

From the first it was easy to recognize Elliot Smith as a student of outstanding quality and of eager interest, and not alone in his professional studies. I cannot remember any special excellence in games or athletic occupations, but already his musical and artistic proclivities were in evidence. His clear gift for decisive black-and-white draughtsmanship, so obvious later in the illustrations of his scientific papers, appears to have been a family quality. It is much less generally known that he was the possessor of a resonant bass voice of quite exceptional quality. He was therefore greatly in request on University social occasions, and I believe that, had he so chosen, he might have had a successful professional musical career.

Although he distinguished himself as a student, even in the ordinary examination tests, he did not appear to seek supremacy in that direction.

In my own Department I soon chose him as one of the Prosectors for the anatomy classes. In this capacity he had ample opportunity to display his interest in human structure and his proficiency in the technique of dissection.

The academic year following his graduation as M.B., Ch.M. was spent in the post-graduate clinical work of hospital house-appointments. In the succeeding year, 1894, he returned to the Department of Anatomy as Demonstrator, and thus began his productive career as an anatomical teacher and investigator.

Here it will be of some interest to take note of several of the men with whom Elliot Smith was associated in those early days.

The University of Sydney of that period was fortunate in the personnel of its junior staff. Whilst Elliot Smith was a student working in the Department of Physiology, Almroth Wright was a Demonstrator, and with him young Elliot Smith developed a lasting friendship. Wright was succeeded in 1891 by C. J. Martin who remained to become a colleague on the University staff during Smith's two years' tenure of the Demonstratorship of Anatomy, 1894–6. Another colleague during this latter period was J. P. Hill, his present colleague in University College, London. There can be no doubt that the stimulating contact with such friends and colleagues as these must have counted for much in Elliot Smith's earlier scientific development.

My own association as Professor with my ten years' younger Demonstrator was of the happiest. From the first days of our connexion he showed himself to be a helpful, enthusiastic and effective teacher; whilst his interest and his initiative in anatomical research developed with astonishing rapidity.

I think that I may assume some credit for guidance of his first steps along the pathways of the literature of anatomical investigation, though not for the choice of the precise problems to which he presently turned his attention. And when once he had entered upon the selected avenue of his first serious research, he was emphatically an independent worker. His originality of mind was impressive and I can even now recall the somewhat disconcerting impact of his fresh reading of some anatomical features of brain structure upon my own perhaps more traditional outlook.

This quality of mind became conspicuous in the very first of his memoirs on brain structure published in the *Proceedings of the Linnean Society of New South Wales* as early as 1894. This paper already contained the germ of the brilliant conception which was later to go far to revolutionize so much of our knowledge of brain morphology, more especially of the rhinencephalon. Some years later, indeed, Edinger, the celebrated Frankfurt neuro-morphologist, referred to this early paper as a "classic".

Towards the close of his tenure as Demonstrator, Elliot Smith obtained the Doctorate of Medicine—the first awarded (apart from an occasional *ad eundem* degree) in the then youthful Sydney Medical School. The degree was awarded on a printed thesis with a supplementary written examination. I still possess the script of the candidate's examination paper, which showed a sure grasp and competent appreciation of various morphological problems offered for critical discussion.

The thesis embodied an important contribution to our knowledge of the anatomy and histology of the brain of the non-placental mammal. In accordance with the University regulations it was presented in printed form and, on the special recommendation of the examiners, a gold medal was awarded. So far as I am aware, the thesis has never been published as such, and I regret to say that my own copy of this interesting document unfortunately disappeared at the hands of a borrower many years ago!

A glance at the bibliography will witness to the strikingly productive activity of the years of Smith's Sydney demonstratorship. Several of these papers are of permanent importance and collectively they represent a notable contribution to the literature of brain morphology. They include papers on the cerebral commissures, on the relation of the olfactory bulb to the hippocampus and on the brain of monotremes and marsupials.

It does not fall within the scope of this brief biographical notice to follow up the progressive development of Elliot Smith's remarkable contribution, both in fact and in interpretation, to the subject of neuro-morphology; still less to touch on his increasing contributions to knowledge in other fields. It must be sufficient to remark that from the outset he showed himself to be not only a scientific observer of keen and penetrating vision, but a master of clear and forcible expression.

It is true that at times his lucid thinking was apt to reach expression in somewhat over-forceful and pungent style, so that those to whom he was personally unknown could hardly be expected to discern the genial and friendly personality underlying the somewhat trenchant language of the acute critic.

It soon became clear that Elliot Smith was meant for a lifework of scientific investigation rather than for the professional life of a medical practitioner. I therefore suggested to him that he should seriously consider the project of taking up anatomical work in Great Britain, where there were wider opportunities for such a career than in Australia.

The first suggestion of such a course did not commend itself to him but a little later he reopened the question and finally resolved to enter upon the adventure proposed.

Fortunately at this juncture a travelling scholarship from the University of Sydney became available and on securing this, in 1896, he left Australia with introductions to various anatomists and others in the British Isles, with whom he soon came into touch. In a letter of September 1896 he records a meeting of the Anatomical Society at Oxford in July, where he met most of the anatomists of Great Britain and Ireland. He also reports visits to the anatomical schools of Edinburgh and Cambridge.

His Cambridge visit proved a fateful one, for there Professor Macalister suggested his entering as a "Research Student"—a status which had only recently been established at Oxford and Cambridge. He found the Oxford requirements for entry to a college "practically prohibitive because a man must become a member of a college in the ordinary way. My Latin and Greek are rather too rusty for that. I therefore gave up all thought of Oxford at once. The Cambridge people are far more rational, and, provided a man is accepted by the Faculty as a 'Research Student' he is admitted *ipso facto* as a College member after producing moral certificates etc." Here Almroth Wright was useful to him, and "now Dr Donald MacAlister has guided me through the devious paths of the college system to a membership of St John's College".

In a later letter (18 November 1896) he writes: "I have now been in Cambridge seven weeks but the time has flown so quickly that I hardly seem to have begun work. I have been working most of the time in the physiological laboratory in a room with H. K. Anderson, who has done a lot of 'sympathetic' work with Langley but who is now launching out on his own account on the sympathetic of the human foetus. He is an awfully good companion but rather burns the candle at both ends in the way of research and teaching. Hardy works in the next room at cell structure. Gaskell who works at his private residence upon his pet subject, and Langley who has little time for anything but teaching, are frequent visitors to our part of the lab.... So far I have done all my work in the physiological laboratory because there are no facilities for doing histological work in the anatomical department. Still I see a good deal of Macalister".

We thus see Elliot Smith more or less established in Cambridge with facilities for carrying on work in his chosen line of anatomical research.

During the three strenuous—not to say struggling—years that followed, his activity was amazing. His output of work included separate researches on the origin of the corpus callosum and on the brain of the Edentata, both published in the *Transactions of the Linnean Society of London*, as well as a series of important papers in the *Journal of Anatomy* on the margin of the cerebral cortex and other features of the mammalian brain. During this period also his laborious work on the preparation of the descriptive catalogue of the brain collection in the Museum of the Royal College of Surgeons was undertaken and partly carried out.

In the year 1899 Elliot Smith was elected into a Fellowship of St John's College, after the lapse of only three years from his entering the College. This exceptional distinction was gained on the strength of a thesis embodying a comprehensive presentation of the results of his recent researches in cerebral morphology.

The award of this Fellowship was an event which may be regarded as marking the close of the earlier phase of Elliot Smith's career as an anatomist and the record of it may fitly end this brief sketch of the initial stages of his development.

I would only add that, in a letter written on 4 July 1900, Prof. Macalister conveyed to Elliot Smith an invitation to become the first occupant of the chair of anatomy in the Government Medical School in Cairo. The acceptance of this offer was destined to involve him, in an unforeseen and unlooked for manner, in a new sphere of scientific and intellectual interests. Elliot Smith perforce became an anthropologist. Yet the imposing bibliographical record of his published work yields abundant evidence of his continued activity as anatomist and neurologist. The Arris and Gale Lectures, in particular, embody his later (1909–10) masterly and illuminating presentation of the essential factors of cerebral evolution and morphology. J. T. W.

THE TERMINATION OF ASCENDING TRACTS IN THE THALAMUS OF THE MACAQUE MONKEY

By W. E. LE GROS CLARK
Department of Human Anatomy, Oxford

It is well known that a large part of the elaborate cerebral cortex of the mammalian brain is concerned with the reception and interpretation of sensory impulses which are relayed to it by the thalamus. The progressive evolution of this cortical structure has formed the main theme of many classical studies by Sir Grafton Elliot Smith, and so far back as the beginning of this century(8) he designated it by the term "neopallium", a term which has now passed into the common language of neurologists. In his Arris and Gale Lectures in 1910(9), Sir Grafton[1] summarized the implications of his earlier researches, and showed how the original mapping out of the neopallium into different morphological and functional areas was determined primarily by the topographical arrangement of the various thalamic nuclei which gave rise to cortical projection fibres. The present problem forms part of a general enquiry into the relation of the thalamus to the cortex in the Primates. In some recent papers(4, 5, 18) the precise arrangement of various thalamo-cortical projection systems has been studied in the macaque monkey by defining the cell atrophy in the thalamic nuclei which follows local cortical ablations. It has now become necessary to determine the source of the afferent fibres which reach these nuclear elements from lower functional levels, with the object of analysing the nature of the impulses which are relayed by them to the neopallial cortex. In the present study, attention has been directed to the precise locus of termination of various ascending tracts from the spinal cord and the brain stem in regard to different nuclei of the thalamus. This question has been partially discussed in the case of lower mammals by Probst(13), Wallenberg(19, 20), Cajal(2), Ranson & Ingram(14), etc., and to a limited extent in the monkey by Vogt(15). In making use of the Marchi method for the study of this problem it may be mentioned that the limitations of this technique are fully realized. Nevertheless it is desirable to ascertain what information it can provide even if some of the conclusions to which it leads may require to be corroborated by other experimental methods.

[1] The stimulus provided by this eminent anatomist in his work as an original investigator, as a teacher, and as an exponent of the problems of Primate evolution, has been justly recognized as a potent factor in the development of neurological anatomy in this country. It would be difficult for the present writer to express how much he owes to this stimulus—it is sufficient to say that he derived the original inspiration for his enquiries into anatomical problems from the lectures and writings of Sir Grafton Elliot Smith, and that he feels it to be a signal honour to contribute to this dedication volume of the *Journal of Anatomy*.

MATERIAL AND METHODS

The ordinary macaque monkey, *Macaca mulatta*, was used for the experimental lesions. The observations recorded here are based on eight experiments, in some of which lesions were made on either side involving different afferent elements. The lesions were distributed over the spinal cord, the medulla, and the mid-brain. The animals were anaesthetized by an intraperitoneal injection of sodium ethyl barbiturate (nembutal), using 0·7 c.c. of a 5 per cent solution per kg. of body weight. Following the operations, the animals were allowed to survive for approximately 12–14 days. They were killed by chloroform anaesthesia followed by an injection through the aorta of 10 per cent formol saline. After 2 hours the brain was removed and cut into slices 2 or 3 mm. in thickness. These were washed for several hours in running water and stained for Marchi degeneration in the usual way. The site of the lesion was in every case serially sectioned and stained either with haematoxylin and eosin or by the Marchi method. Serial sections were prepared through the whole length of the thalamus, every fourth section being preserved and mounted. In the study of these sections, the distribution of osmic-stained degenerating fibres in relation to the different thalamic nuclei was carefully mapped out. In all cases the identification of these fibres as truly undergoing Marchi degeneration could be established beyond doubt, for they were usually cut slightly obliquely and in each section they could thus be traced for a short distance along their length. In some instances the sections were quite free of pseudo-Marchi reaction, and here the fine stippling of certain elements of the thalamus with Marchi granules made it possible to define the actual site of the terminal breaking up of degenerating tracts with considerable assurance. In other experiments there was a certain degree of pseudo-Marchi deposit which obscured this stippling. In these cases the degenerating fibres were traced as far as they could be certainly identified, and the precise area of their termination was approximately judged to be in the region where they finally disappeared. In the diagrams illustrating the experiments, the distribution of recognizable degenerating fibres is indicated by interrupted lines, while in those cases in which the sections were sufficiently excellent to allow areas of terminal stippling to be defined, these areas are indicated by dots. The sections illustrated were traced out with a projection apparatus. In Marchi material the outlines of many of the thalamic nuclei (though faintly marked) could be readily detected, as, for instance, the dorso-medial, centre median, arcuate and anterior nuclei, and element *La* of the lateral nucleus. On the other hand, the boundary between the main part of the lateral nucleus (element *Lb*) and the pars externa of the ventral nucleus could not be accurately defined. In any case these nuclei merge into each other with no intervening medullary lamina though their limits can be approximately determined by cyto-architectural and myelo-architectural features. As has been recently shown, also, they can be differentiated by their cortical connexions, for while the pars externa of the ventral

nucleus projects entirely on to the area postcentralis, the lateral nucleus (in its caudal part) projects on to the parietal association areas of the cortex (5, 18). In the diagrams in this paper, the approximate boundary between the pars externa of the ventral nucleus and the lateral nucleus has been estimated by comparison with large numbers of Nissl sections cut at equivalent transverse levels (which are available in this laboratory), and by comparison with various atlases of the thalamus of the monkey which have been published. Of these atlases, by far the best is to be found in the magnificent series of microphotographs of Nissl sections reproduced in a paper by Friedemann (10), and this has been extensively used in the present study. The myelo-architecture of the cercopitheque thalamus has been illustrated in a similar way by Vogt. More recently the cyto-architecture of the macaque thalamus has been figured photographicall by Grünthal (11) who, however, uses an unfamiliar nomenclature and has made the confusing error of mistaking the centre median nucleus for the arcuate nucleus. Descriptions of the nuclear configuration of the macaque thalamus have been published in America by Crouch (7) and Aronson & Papez (1), but these are illustrated by hand-drawn diagrams which, however excellent in themselves, are much less useful for purposes of reference and comparison.

EXPERIMENTAL RESULTS

Experiment A. O.M. 83. Operation 13 September 1935, killed 27 September 1935.

A local lesion was made in the right gracile nucleus of this monkey. The medulla was exposed by a laminectomy of the first three cervical vertebrae and a partial removal of the occipital bone behind the foramen magnum. The gracile tubercle was readily identified and the lesion produced by a fine ophthalmic knife. The animal made an uninterrupted recovery.

Histological examination of the lesion

Serial sections were cut through the whole extent of the lesion and stained with haematoxylin and eosin. At the level of the upper limit of the pyramidal decussation, the lesion can be seen extending into the right gracile nucleus, cutting off approximately the medial half of the nucleus (Fig. 1 A). Further up, at the level of the lower end of the fourth ventricle, the lesion extends ventro-medially as far as the lateral margin of the dorsal vagal nucleus and the dorsal margin of the fasciculus solitarius, but if there is any involvement of these structures, it is so slight as to be practically insignificant. At the level of the vascular area postrema, the lesion begins rapidly to diminish and in a few sections disappears entirely. The cuneate nucleus or the arcuate fibres which arise in it are not touched by the lesion.

Course of degenerating fibres

Sections through the pons show marked degeneration localized to the fibres in the lateral half of the medial fillet of the left side. At the level of the mid-brain, the degenerating fibres can be traced up in the lateral end of the fillet, and form a conspicuous bundle lying immediately medial to the medial

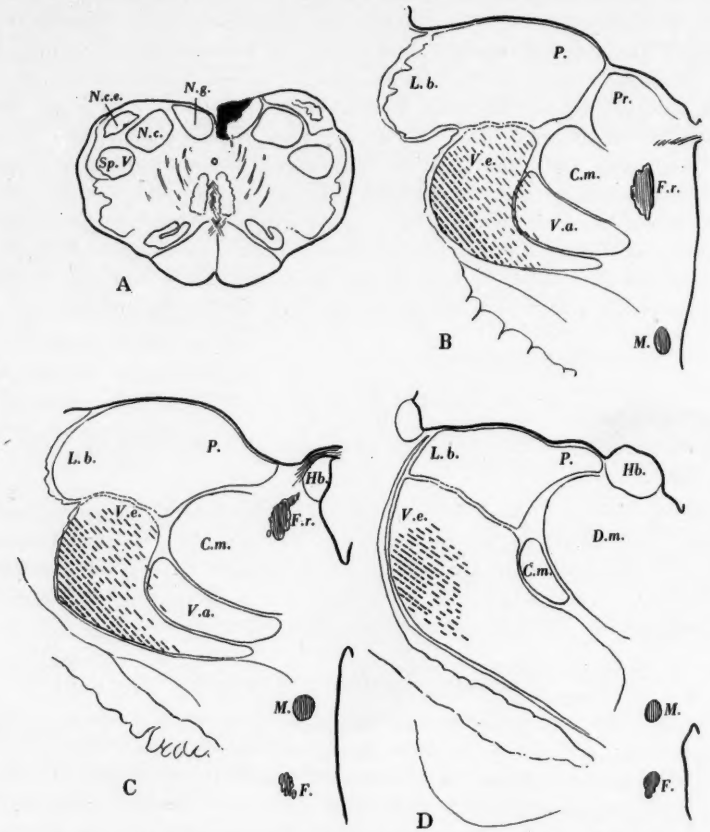


Fig. 1. The lesion and the distribution of degenerating fibres in the thalamus in experiment A (O.M. 83). In this and the following illustrations, the drawings have been made from sections by means of a projection apparatus.

geniculate body. The fibres, which here are cut obliquely, all stream in a lateral direction as they run forwards to reach the caudal limit of the thalamus. No degenerating fibres pass dorsally along the line of the nucleus limitans as they do to some extent after lesions involving the cuneate nucleus or its

arcuate fibres. Degenerating fibres are also completely absent in the medial geniculate body, pulvinar, or in the superior colliculus and its commissure.

In the main part of the thalamus, there is a certain amount of pseudo-Marchi deposit in this specimen. This can be readily distinguished in the sections from the true Marchi degeneration shown by dense osmic staining of fibres which are cut obliquely in their course, but it raises some difficulty in delimiting the zone in which the diffuse sprinkling of osmic granules usually defines the site of actual termination of degenerating fibres. In tracing the course of the affected fibres in the thalamus, therefore, attention has been confined to the fibres themselves, up to the point where they disappear as recognizable fibres. However, the area of actual termination is in fact indicated fairly strongly by the rich network which the degenerating fibres make in the ventral nucleus of the thalamus.

At the caudal end of the thalamus (Fig. 1 B), the degenerating fibres are seen crowding into the lateral half of the pars externa of the ventral nucleus. They are also present throughout this nucleus, but in the medial half they are scattered and appear to be fibres of passage making their way laterally. The arcuate nucleus (pars arcuata of the ventral nucleus) is quite free of degenerating fibres except at its lateral margin, and here the few isolated fibres showing osmic staining which are present are clearly fibres of passage. No degenerating fibres run over the arcuate nucleus in the intermediate medullary lamina as is the case with some of the fillet fibres which take origin from the cuneate nucleus. The lateral nucleus, centre median nucleus, and the dorso-medial nucleus are all entirely free of degenerating fibres. Traced forwards, the fibres gradually disappear from the medial half of the pars externa of the ventral nucleus. The lateral half of the nucleus becomes more crowded with a network of osmic-stained fibres, scattered in among which are numerous coarse Marchi granules. At the level of the rostral end of the centre median nucleus, degenerating fibres are only to be found in the lateral part of the ventral nucleus where they are limited to an area lying close against the lateral medullary lamina (Fig. 1 D). In front of the anterior end of the centre median nucleus, no more Marchi degeneration is to be seen.

It is clear from this experiment that fillet fibres from the gracile nucleus are destined for the most lateral part of the pars externa of the ventral nucleus. Many of these fibres reach this area from below by running laterally in the ventral medullary lamina of the thalamus, while others approach it from the medial aspect by running through the medial half of the pars externa.

Experiment B. *O.M.* 86. Operation 19 September 1935, killed 2 October 1935.

In this experiment a lesion was made in the cuneate nucleus on the left side, and the spinal nucleus of the fifth nerve on the right side. The medulla was exposed by a laminectomy of the upper three cervical vertebrae, and removal of part of the occipital bone. The animal made a rapid recovery.

Histological examination of the lesions

Right side. At the level of the lower margin of the pyramidal decussation the lesion can be seen entering the superficial aspect of the spinal nucleus of the fifth nerve. It cuts through the middle of the nucleus in a ventro-medial direction to reach its ventro-medial angle (Fig. 2 A). The lesion thus interrupts the fibres which run medially from the ventro-lateral half of the lower part of the nucleus. The lesion extends up to the level of the lower angle of the fourth ventricle, where it extends ventrally as far as the margin of the dorsal spino-cerebellar tract.

Left side. As the sections are traced rostrally, the lesion on this side is first seen entering the termination of the fasciculus cuneatus at the level of the lower extremity of the fourth ventricle. Further up it extends ventro-medially, involving the dorsal part of the external cuneate nucleus (Fig. 2 B). Still more rostrally (Fig. 2 C), the lesion extends inwards to involve the cuneate nucleus proper (the pars triangularis as defined by Ferraro and Barrera).

On both sides, the lesions are strictly localized.

Course of degenerating fibres

Right side. Sections through the medulla, pons, and mid-brain stained with osmic acid show numerous coarse degenerating fibres scattered throughout the right medial fillet, the result of the lesion involving the left cuneate nucleus. At the caudal end of the thalamus, the majority of these fibres turn dorso-laterally and stream into the pars externa of the ventral nucleus in this direction. A few run dorsally along the line of the nucleus limitans (Fig. 3 A). At the level of the caudal extremity of the arcuate nucleus, the fibres mainly skirt the margin of this nucleus on their way dorso-laterally; some, however, can be seen as separate and isolated fibres running through the nucleus. It seems certain that these are fibres of passage only, for they can be traced laterally in the serial sections into the pars externa of the ventral nucleus, and, unlike the latter, the groundwork of the arcuate nucleus is free of osmic sprinkling. At the caudal end of the pars externa degenerating fibres are already breaking up into a terminal network in this nucleus (Fig. 3 A). It may be noted that no Marchi degeneration is present in the pulvinar, in the lateral nucleus, or in the posterior commissure. At the transverse level of the maximum development of the centre median nucleus, most of the medial half of the pars externa is filled with numerous degenerating fibres. Along the medial border of the nucleus and at its ventro-medial extremity, these appear to be fibres of passage only. The actual site of termination is indicated by a rich deposit of Marchi granules concentrated in a vertical zone in the middle of the nucleus (Fig. 3 B). At this level the arcuate nucleus is devoid of osmic staining except at its margins and its dorso-lateral extremity, where isolated fibres of passage are present in small numbers. Further rostrally, the dorso-lateral extremity of the arcuate nucleus becomes free of degenerating fibres which have by this level passed into the

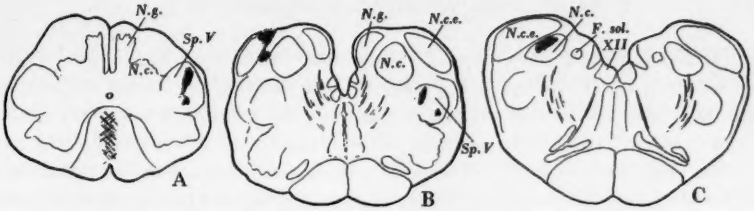


Fig. 2. The lesions in the medulla in experiment B (O.M. 86).

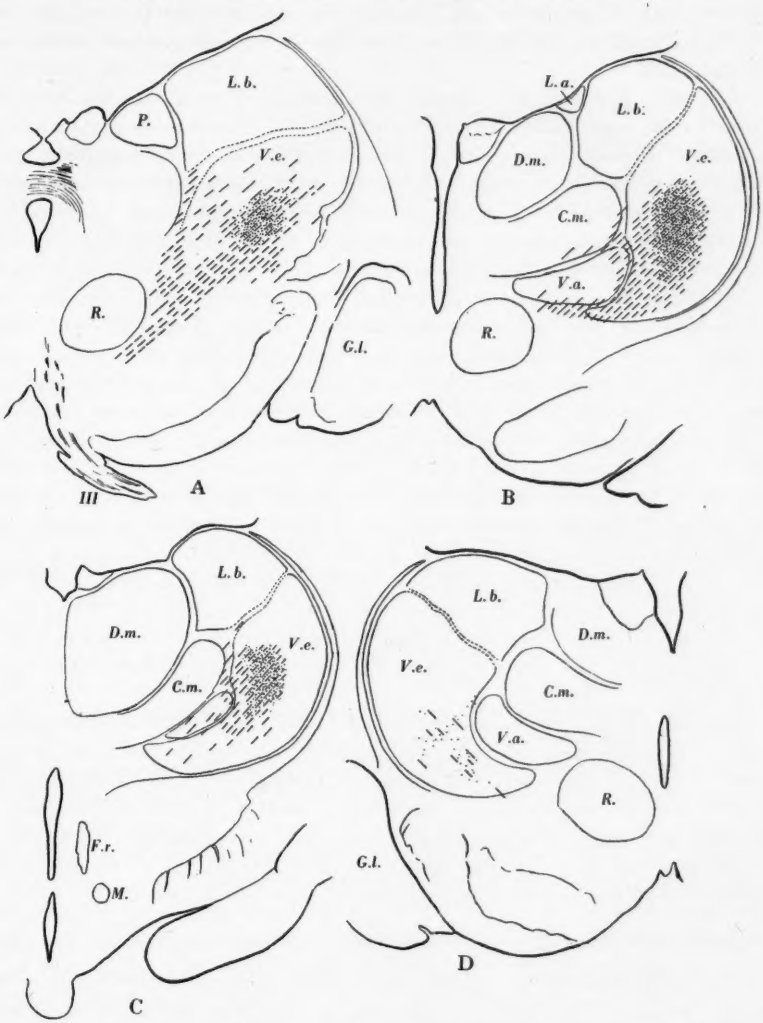


Fig. 3. The distribution of degenerating fibres in the thalamus in experiment B (O.M. 86).

medial aspect of the pars externa. The centre median nucleus is also free of degenerating fibres, though a few may be seen skirting its lateral and ventral margins in the intermediate medullary lamina. In sections through the middle of the thalamus, degenerating fibres are confined to the medial half of the pars externa (Fig. 3 C). Again, the area of termination appears to be a zone near the middle of the nucleus, the medial margin and ventral extremity containing fibres of passage only. At the level of the rostral end of the centre median nucleus, that is, approximately mid-way between the posterior commissure and the anterior limit of the thalamus, no Marchi-stained fibres are present on the right side.

Left side. Although it is certain from a study of serial sections that the lesion on the right side must have interrupted a considerable proportion of secondary neurones arising in the lower half of the spinal nucleus of the trigeminal nerve, it has produced extremely little degeneration in the sensory tracts which ascend to the thalamus on the left side. There are indeed a few Marchi granules scattered in the medial fillet of this side, and also a few in the central tegmental fasciculi, which certainly indicate in these sections degenerating fibres. In sections through the mid-brain, where the fibres of the medial fillet are cut somewhat obliquely as they begin to turn dorso-laterally, a few of them seem definitely to be undergoing degeneration, and here, also, one or two fibres stained with osmic acid can be seen running into the deeper layers of the superior colliculus. At the caudal end of the thalamus, a few isolated and fine degnerating fibres are present in the ventro-medial end of the pars externa of the ventral nucleus (extending laterally from the position of the nucleus limitans), and over a small area here there is a diffuse scattering of Marchi granules which is sufficiently distinct to suggest the termination in this region of a small number of degenerating fibres (Fig. 3 D). This area of slight osmic staining can be traced forwards in serial sections to the level of the rostral extremity of the centre median nucleus. There is no Marchi deposit in the arcuate nucleus, centre median nucleus or dorso-medial nucleus, nor are any degenerating fibres present in the periventricular grey matter.

The results of this experiment indicate that the cuneate nucleus (which receives impulses from the upper extremity and the upper part of the trunk), projects on to a zone extending along the middle of the pars externa of the ventral nucleus. On the other hand, the projection of the spinal nucleus of the fifth nerve on to the thalamus appears to be very slight indeed, and is confined to the medio-ventral end of the pars externa (i.e. to an area lying medio-ventral to the area of termination of the cuneate fibres).

Experiment C. O.M. 104. Operation 15 October 1935, killed 29 October 1935.

In this experiment the intention was to make a circumscribed lesion in the spinal nucleus of the trigeminal nerve on the right side, and in the medullary nucleus on the left side. The medulla was exposed by removing the laminae

of the first three cervical vertebrae and also the lower part of the occipital bone. On opening the spinal theca, the tubercle of Rolando was identified and provided a landmark for the spinal nucleus. A lesion was produced with a small curved ophthalmic knife. The vermis of the cerebellum was then retracted upwards and the cavity of the fourth ventricle exposed. The knife was passed up towards the lateral recess and allowed here to penetrate the medulla in a direction which was judged to reach the medullary nucleus of the trigeminal nerve.

The animal made a rapid and uneventful recovery, and showed no ascertainable effect of the lesions.

Histological examination of the lesions

Sections through the lower part of the medulla, at the level of the pyramidal decussation, show the site of the lesion marked by two small patches of fibrosis in the spinal nucleus of the fifth nerve on the right side (Fig. 4 A).

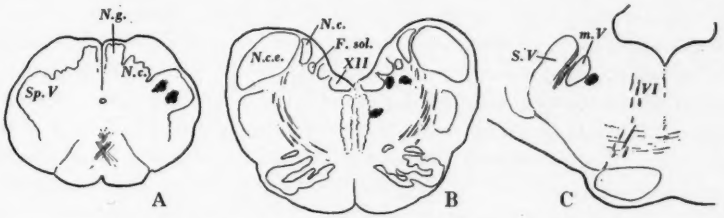


Fig. 4. The lesions in the medulla in experiment C (O.M. 104).

At this level no other parts of the medulla are involved. Further rostrally, the lesion extends medially, reaching the margin of the cuneate nucleus and involving some of the fibres of the sensory decussation which issue from it. At the level of the lower end of the fourth ventricle the lesion extends medially immediately below the hypoglossal nucleus, severing here the lemniscus fibres from the upper end of the gracile and cuneate nuclei. Still further rostrally, the lesion is marked by three separate patches of fibrosis, of which one lies immediately below the hypoglossal nucleus and close against the lateral margin of the medial lemniscus and the posterior longitudinal bundle, involving a few fibres of these tracts (Fig. 4 B). The other patches lie immediately below the dorsal vagal nucleus and the solitary bundle.

The serial sections show that the lesion on the left side was situated too medially to reach the main sensory nucleus of the fifth nerve, and a little too dorsally to involve the arcuate fibres from either the spinal or the main sensory nucleus. At its lower extremity, the lesion lies immediately below the position of the medial vestibular nucleus, here interrupting fibres running medially from this nucleus to the posterior longitudinal bundle. Further rostrally it cuts through the ascending limb of the intramedullary root of the facial nerve.

At its extreme upper end the lesion reaches to the level of the central origin of the sixth nerve, here lying medial to the motor nucleus of the fifth nerve, but unfortunately a little dorsal to the arcuate fibres from the main sensory nucleus (Fig. 4 C).

On the right side, then, the lesion involves the lower end of the spinal nucleus of the fifth nerve, a proportion of the lemniscus fibres coming from the upper end of the cuneate nucleus, and, to a lesser extent, of the gracile nucleus, and also a few of the crossed fibres of the medial lemniscus of this side. On the left side, the lesion unfortunately misses any part of the lemniscus system.

Course of degenerating fibres

Left side. Sections through the mid-brain, at the level of the upper border of the pons, the superior colliculus and the medial geniculate body, show well-marked degeneration throughout the medial fillet which arises from the lesions in the right side of the medulla. Scattered degeneration is also present in the central tegmental fasciculi close to the central grey matter around the aqueduct. This degeneration occupies the position of the dorsal secondary trigeminal path described by Wallenberg, but in this experiment it may be derived from interruption of fibres lower down by the lesion in the left half of the medulla. Isolated fibres showing marked degeneration run dorsally from the central tegmental fasciculi to course round the central grey matter, and a few of these fibres enter this grey matter. On both sides, and especially on the right, there is scattered degeneration in the posterior longitudinal bundle (probably resulting from interruption by the lesion of fibres from the medial vestibular nucleus), and a fine network of degenerating fibres extends from the bundle into the oculomotor nucleus. A few isolated degenerating fibres are definitely present in the commissure of the superior colliculus, apparently derived from the central tegmental fasciculi of the left side. Further rostrally, the degenerating fibres of the medial fillet may be divided into two main groups, of which the more medial now begin to stream dorso-laterally along the line of the nucleus limitans, while the more lateral and denser part forms a fairly compact bundle immediately medial to the medial geniculate body. At least some of the more medial fibres run dorsally into the deeper layers of the superior colliculus. There is complete absence of osmic staining in the pulvinar, medial geniculate body and posterior commissure. Sections through the caudal part of the thalamus show numerous degenerating fibres ending in the greater part of the pars externa of the ventral nucleus, except for its most dorsal part (Fig. 5 A). The degeneration is rather less dense in the lateral margin of the nucleus. Not only are abundant fibres showing the osmic staining, and cut obliquely, seen coursing dorso-laterally in the pars externa, but the ground substance of this nucleus is richly sprinkled with osmic granules, indicating the actual termination of degenerated fibres therein. Some of the more medial fibres of the medial fillet enter the intermediate medullary lamina which forms the lateral boundary of the centre median nucleus, and a few run through the

caudo-lateral extremity of this nucleus. By tracing the serial sections forwards, these fibres can be followed laterally eventually to end in the dorso-medial part of the pars externa of the ventral nucleus. Moreover, the centre median nucleus contains no sprinkling of osmic granules which might indicate a terminal breaking up of degenerating fasciculi, and the greater part of the nucleus

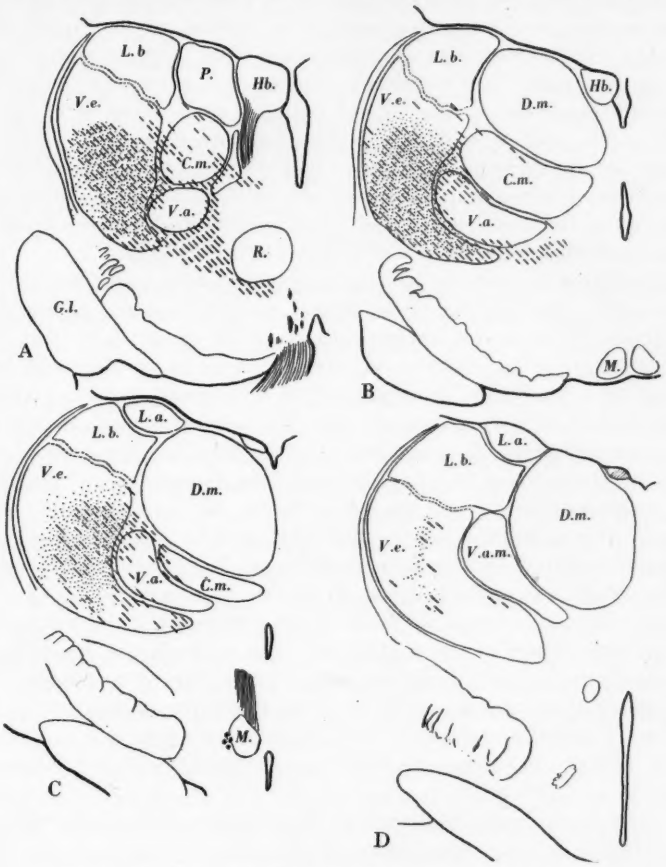


Fig. 5. The distribution of degenerating fibres in the thalamus in experiment C (O.M. 104).

is quite free even of degenerating fibres of passage. At the caudal part of the thalamus, the pars arcuata of the ventral nucleus appears. Again, isolated fibres showing osmic staining are evident, passing through the caudal extremity of this nucleus, but a careful study indicates that they are fibres of passage only, running dorso-laterally to reach the pars externa of the ventral nucleus.

As the sections are traced forwards, the medio-ventral part of the arcuate nucleus becomes free of degenerating fibres.

Towards the middle of the thalamus, the degenerating fibres in the pars externa of the ventral nucleus diminish rapidly, and at this level the lateral part of the nucleus is free of osmic deposit (Fig. 5 C). Finally, at the level of the caudal border of the optic chiasma, only very few isolated fibres are evident, and osmic granules in the groundwork of the nucleus are very inconspicuous (Fig. 5 D). Further rostrally, no degenerating fibres are to be seen.

It may be noted that no Marchi degeneration is present in the lateral nucleus, the dorso-medial nucleus, the nuclei of the mid-line or in the hypothalamus. The medial medullary lamina (circumscribing the dorso-medial nucleus) contains no degenerated fibres except at its posterior end, where one or two isolated fibres of passage are passing laterally between the caudal extremities of the dorso-medial and centre median nuclei to reach the intermediate medullary lamina.

On the left side, then, the degenerating fibres which arise from the lesions involving the spinal nucleus of the fifth nerve and a part of the medial lemniscus fibres appear to end entirely in the pars externa of the ventral nucleus. If any terminate in the centre median or arcuate nuclei, they are very few and are confined to the caudal extremity of the former and the dorso-lateral extremity of the latter. But, as pointed out, the sections indicate that these are almost certainly fibres of passage only. The fact that the dorsal part and most of the lateral margin of the pars externa of the ventral nucleus are also free of degenerating fibres, is perhaps related to the fact that the lesion involves predominantly the fifth nucleus and fibres from the cuneate nucleus, whereas only very few of the lemniscus fibres from the gracile nucleus (bringing impulses from the caudal end of the body) could have been interrupted.

Right side. A few scattered fibres showing Marchi staining are present in the most lateral part of the medial fillet, and these can be traced rostrally to terminate in the most lateral part of the pars externa of the ventral nucleus. This degeneration probably results from the slight involvement of the crossed fibres at the lateral margin of the medial fillet of the right side as already described. No other elements of the thalamus on this side show any degenerating fibres.

In no sections could degenerating fibres be found in the periventricular grey matter of the third ventricle on either side.

Experiment D. O.M. 59. Operation 1 October 1935, killed 15 October 1935.

A lesion was made in the floor of the fourth ventricle on the left side in an attempt to reach the medullary nucleus of the fifth nerve. The fourth ventricle was approached by the sub-occipital route, the cerebellum being raised in order to expose the lower part of its floor.

Serial sections were taken through the medulla, but unfortunately they only show the rostral end of the lesion, for the latter had not reached so far

forwards as had been intended. Thus it is not possible in this experiment to state the precise extent of the medullary lesion. Since the Marchi sections show abundant degeneration throughout the medial fillet of the right side, it is quite evident that the decussating fibres from the rostral ends of the cuneate or gracile nuclei (or both) must have been involved. The lowest of the serial sections shows the anterior end of the lesion extending ventrally and slightly medially into the medulla to reach a point approximately mid-way between the ventral border of the descending nucleus of the fifth nerve and the medial plane (Fig. 6 A). Thus this part of the lesion interrupts some of the arcuate fibres of the trigeminal fillet from the descending nucleus, and also some of the fibres forming the central tegmental fasciculi. The rostral end of the lesion is at the level of the lower end of the facial nucleus. The medullary nucleus of the fifth nerve is intact.

Course of degenerating fibres

Sections through the mid-brain at the level of the anterior colliculus show degenerating fibres strewn throughout the width of the medial fillet on the right side, rather more densely in the lateral half. There is no osmic staining in the fibres of the left medial fillet. There is also scattered degeneration in the central tegmental fasciculi of both sides. This is quite definite, and some of the affected fibres may be seen, cut obliquely along their length, radiating dorsally from the fasciculi towards the colliculus. The degenerating fibres in the tegmental fasciculi of the right side are evidently the result of the interruption of the arcuate fibres from the descending nucleus of the fifth nerve on the left side, and mark the course of the secondary trigeminal path in the tegmental region which was originally described by Wallenberg. On the left side the degeneration is due to the interruption of these tegmental fibres on the same side at a lower level by the lesion.

Degenerating fibres from the central tegmental fasciculi can be traced on both sides in among the cells of the mesencephalic nucleus of the fifth nerve, a few also extending into the central grey matter around the cerebral aqueduct. Others run dorsally into the commissure of the anterior colliculus, where they cross the mid-line, or into the deeper layers of the colliculus. Further rostrally, some extend upwards and forwards along the line of the nucleus limitans.

As the affected fibres of the right medial fillet are traced rostrally, they are seen to run in well-defined fasciculi in a dorso-lateral direction on the lateral aspect of the red nucleus—between it and the anterior end of the medial geniculate body. From here, they stream laterally into the caudal end of the pars externa of the ventral nucleus, the medial portion of which they fill (Fig. 6 C). Immediately adjacent to the anterior end of the medial geniculate body the network of degenerating fibres is particularly dense, and here the groundwork is scattered with osmic granules indicating the termination in this area of the fillet fibres. Further dorsally, on the right side, there is a slight concentration of degenerating fibres in the intermediate medullary lamina at

the caudal pole of the centre median nucleus, while a few isolated fibres are also to be seen penetrating the nucleus parafascicularis close alongside the fasciculus retroflexus. Where the posterior pole of the arcuate nucleus first

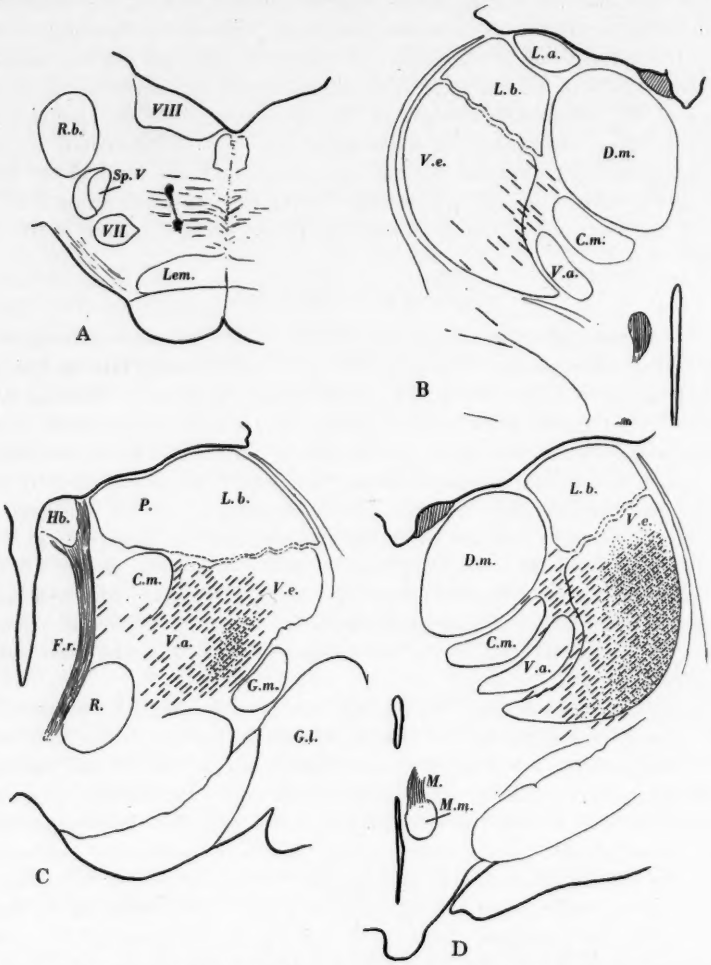


Fig. 6. The rostral end of the lesion, and the distribution of degenerating fibres in the thalamus in experiment D (O.M. 59).

becomes recognizable, the degenerating fillet fibres for the most part skirt its margins on their way to more rostral levels of the pars externa of the ventral nucleus. Further forwards, at the level of the mammillary bodies and the tuber cinereum, the pars externa is practically filled throughout its extent in coronal

section by Marchi-stained fibres (Fig. 6 D). This network is more dense towards the lateral and dorsal parts of the nucleus, and in these regions the profuse sprinkling with osmic granules suggests that most of the fibres terminate. The lateral nucleus throughout is quite free of osmic staining. These sections are particularly instructive in showing an abrupt transition between the clear zone of the lateral nucleus above and the Marchi-sprinkled area of the ventral nucleus below. On the right side most of the degenerating fibres enter the pars externa of the ventral nucleus from the ventral medullary lamina below. Some, however, which are probably mainly derived from the central tegmental fasciculi of the brain stem, run through the ventral part of the medial medullary lamina, and the intermediate medullary lamina, to enter the pars externa from the medial aspect. The degeneration in the pars externa of the right side extends forward as far approximately as the middle of the thalamus. It may be noted that, on the right side, the centre median and arcuate nuclei are free of Marchi staining except for isolated fibres of passage at their posterior extremities, while the dorso-medial nucleus is entirely clear throughout its extent.

On the left side a moderate number of degenerating fibres can be seen extending into the pars externa of the ventral nucleus, the result of the involvement by the lesion of the secondary trigeminal paths in the central tegmental fasciculi of the same side (Fig. 6 B). They reach the caudal part of the thalamus by passing for the most part through the parafascicular nucleus. From here they radiate laterally into the ventro-medial extremity of the caudal end of the pars externa, while others run forwards into the ventral part of the medial medullary lamina and the capsule of the centre median nucleus to reach the medial margin of the pars externa further rostrally. In this relative position, the degenerating fibres reach forwards to the level of sections passing through the caudal margin of the optic chiasma. No degenerating fibres on the left side are found to end in the centre median, arcuate, dorso-medial or lateral nuclei.

Experiment E. O.M. 80. Operation 11 September 1935, killed 23 September 1935.

In this case a hemisection of the spinal cord was made on the left side between the fourth and fifth cervical nerve roots. The animal made a rapid recovery from the immediate effects of the operation, showing complete paralysis of the left arm and leg. Following the operation, it remained very quiet and huddled up, and could only be persuaded to take nourishment with difficulty. The post-mortem examination showed that the lesion was entirely local and uncomplicated by sepsis or haemorrhage. Serial sections were taken through the site of the lesion, demonstrating that the hemisection was complete and did not extend across the mid-line.

Course of degenerating fibres

Sections through the spinal cord above the level of the lesion show complete Marchi degeneration of the posterior columns, and considerable degeneration in the more superficial parts of the lateral and ventral funiculi. In the medulla,

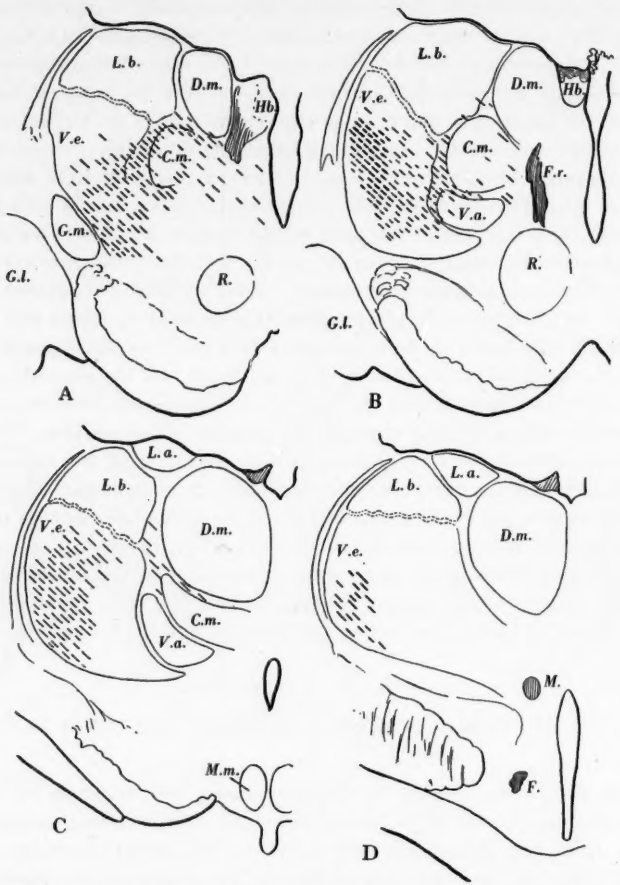


Fig. 7. The distribution of degenerating fibres in the thalamus following hemisection of the spinal cord in experiment E (O.M. 80).

the termination of the posterior column fibres in the cuneate and gracile nuclei is to be observed, the spino-cerebellar tracts are clearly marked out, while the spino-tectal and spino-thalamic tracts (whose identity can be determined by tracing their subsequent course in the serial sections) lie on a deeper plane, ventral to the spinal nucleus of the fifth nerve. At the lower end of the medulla

degenerating fibres, well-stained with osmic acid, occasionally leave these tracts and run dorso-medially to reach the grey matter around the central canal. At a slightly higher level, the spino-thalamic and spino-tectal fibres lie latero-dorsal to the inferior olive, between it and the spinal nucleus of the fifth nerve. They are not sharply separated here from the ventral spino-cerebellar tract. Some fibres penetrate into the inferior olive from its latero-dorsal aspect, while others are observed running at intervals dorso-medially to reach the central grey matter, some of these passing transversely through the medial fillet and crossing over the mid-line. At the level of sections through the pons and upper part of the fourth ventricle, the ventral spino-cerebellar tract is a very conspicuous structure as its degenerating fibres run up over the surface of the brachium conjunctivum. Immediately deep to it and dorsal to the lateral extremity of the medial fillet are the spino-thalamic and spino-tectal fibres. There is no certain evidence of Marchi degeneration in the central tegmental fasciculi, nor is there any degeneration in the medial fillet. At the level of the posterior colliculus many degenerating fibres of the spino-thalamic and spino-tectal tracts run upwards and forwards among and deep to the fibres of the lateral fillet, reaching from a point dorsal to the lateral end of the medial fillet as far as the ventro-lateral margin of the nucleus of the posterior colliculus. Immediately below the latter, a number of well-stained fibres run medially, penetrating the mesencephalic tract and nucleus of the fifth nerve, to reach the central grey matter round the cerebral aqueduct. Some of these degenerating fibres can be traced very distinctly into a sub-ependymal position, where their termination is apparently indicated by a copious sprinkling of Marchi granules on the left side. A considerable number of fibres also skirt the caudal margin of the posterior colliculus, and cross over the mid-line above the aqueduct in the commissure of the posterior colliculus. At the level of the anterior colliculus the spino-thalamic tract is seen as a conspicuous bundle of Marchi-stained fibres lying under cover of the caudo-lateral margin of the colliculus and immediately deep to the inferior brachium. A few degenerating fibres (comprising the spino-tectal component) run dorsally into the deeper layers of the colliculus, and some of these cross over the aqueduct in the commissure of the anterior colliculus.

Sections through the caudal end of the thalamus show that most of the spino-thalamic fibres enter the thalamus in the position of the nucleus parafascicularis and in the area between the latter and the medial geniculate body, somewhat dorsal, therefore, to the entry of the majority of medial lemniscus fibres. The parafascicular nucleus is richly strewn with degenerating fibres, and from this position they radiate in different directions. The bulk of the fibres course laterally, dorso-laterally or ventro-laterally, in order to enter the pars externa of the ventral nucleus (Fig. 7 A). Others run into the intermediate medullary lamina surrounding the centre median nucleus; a few run through the caudal end of this nucleus, but it is doubtful whether they end here. A few fibres also extend into the medial medullary lamina, lateral to the ventral

half of the dorso-medial nucleus. Lastly, at the caudal end of the thalamus, a small number of quite distinct fibres undergoing Marchi degeneration are to be seen in the periventricular grey matter medial to the plane of Meynert's bundle, and they apparently reach this region by running dorso-medially from a more lateral position. In front of the plane of the habenulo-peduncular tract, no degenerating fibres are to be seen near the ventricle. Further forwards, almost the whole of the pars externa of the ventral nucleus is permeated with coarsely degenerating fibres. They are rather more conspicuous towards the lateral half of this nucleus and, in this position, mainly run dorsally and laterally. At the level of the mammillary bodies, they are almost entirely collected in the lateral half of the pars externa (Fig. 7 C). At the level of infundibulum and the caudal margin of the optic chiasma they are limited to its ventro-lateral angle, and they can be traced forward in this position almost as far as the transverse plane of the caudal margin of the anterior nucleus of the thalamus.

It is evident that the great bulk of the degenerating fibres of the spino-thalamic tract terminate in the pars externa of the ventral nucleus, probably ending in all parts (as far forwards as approximately the rostral border of the centre median nucleus) except the medio-ventral region. Unfortunately, in this specimen, there is some pseudo-Marchi staining in the thalamus which makes it too difficult to determine the precise site of the breaking up of fibres of termination by reference to diffuse osmic stippling. However, fibres undergoing true Marchi degeneration can be distinguished readily enough, and the appearance of the network of these fibres does give some indication of the site of their termination. It has been noted that some degenerating fibres enter the medial and intermediate medullary lamina. These can be traced forwards as far as the level of the anterior extremity of the centre median nucleus. Many of them run forwards through the nucleus centralis lateralis. Those in the ventral half of the medial medullary lamina are cut obliquely, and they are seen to be directed dorso-laterally. Their destination is uncertain, for they lie too far dorsally to be aiming for the ventral nucleus, and they certainly cannot be traced into the lateral or dorso-medial nucleus. The impression is gained that these fibres probably end in the intra-laminar nuclei corresponding to the medial and intermediate medullary lamina, and including the nucleus centralis lateralis.

The pars arcuata of the ventral nucleus is empty of degenerating fibres except for the lateral part of its caudal extremity, and here the fibres are probably passing through on their way to the pars externa and the intermediate medullary lamina. The same applies to the centre median nucleus which is also clear of degenerating fibres for the most part. Further, it may be noted that no fibres undergoing Marchi degeneration can be found in the pulvinar, the lateral nucleus, or the dorso-medial nucleus.

Experiment F. O.M. 127. Operation 26 February 1936, killed 10 March 1936.

In this experiment a hemisection of the spinal cord was made between the third and fourth thoracic segments. The animal made a good recovery. Serial

sections were taken through the lesion and showed that the hemisection was complete and limited strictly to the left side of the cord.

Course of degenerating fibres

Sections through the cervical part of the spinal cord show that the fibres of Goll's tract on the left side have undergone well-marked Marchi degenera-

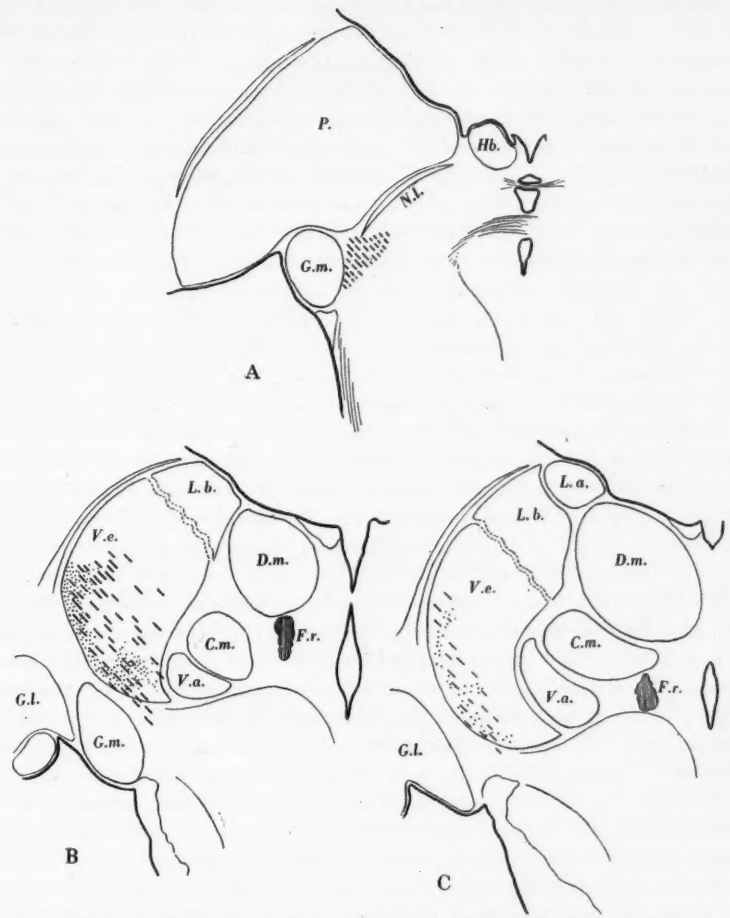


Fig. 8. The distribution of degenerating fibres in the thalamus following hemisection of the cord in experiment F (O.M. 127).

tion. Degeneration also extends over the peripheral part of the lateral and ventral funiculi, involving the spino-cerebellar and the spino-thalamic and spino-tectal tracts. On the right side there are scattered degenerating fibres

in the same regions, but these are very few and inconspicuous. Sections through the medulla at the level of the pyramidal decussation show degenerating fibres ramifying in the gracile nucleus and in the extreme medial corner of the cuneate nucleus on the left side. At the level of the middle of the inferior olive, the fibres of the dorsal spino-cerebellar tract are seen running into the restiform body. The spino-tectal and spino-thalamic fibres here lie near the surface of the medulla immediately dorsal to the lateral part of the olive, and cannot at this level be distinguished from the ventral spino-cerebellar tract. In sections through the mid-brain, a mass of degenerating fibres can be seen coursing up in the lateral fillet. These are spino-thalamic and spino-tectal fibres. While a few of them evidently terminate in the nucleus of the posterior colliculus, the great majority skirt the ventro-lateral margin of this nucleus, and continue rostrally as a fairly compact bundle immediately medial and slightly dorsal to the inferior brachium. One or two osmic-stained fibres run medially below the anterior margin of the posterior colliculus and can be traced into the margin of the central grey matter of the aqueduct. Others extend into the deeper layers of the anterior colliculus.

The spino-thalamic fibres which have been interrupted in this experiment enter the thalamus from a position immediately medial to the medial geniculate body (Fig. 8 A). From here they extend up slightly alongside the lower end of the nucleus limitans, and then turn laterally over the rostral pole of the medial geniculate body to enter the caudal extremity of the pars externa of the ventral nucleus by way of the ventral medullary lamina. Thus they appear all to enter this nucleus from the ventral aspect. The pars arcuata of the ventral nucleus and the centre median nucleus are free of osmic deposit, nor is there any certain evidence of degenerating fibres in the parafascicular nucleus or in the periventricular grey matter. At the level of sections passing through the caudal end of the lateral geniculate body and the middle of the medial geniculate body, degenerating fibres are scattered through the ventral half of the pars externa, but they are mainly concentrated here along its ventral and lateral borders (Fig. 8 B). In this region of the pars externa there is a pronounced stippling of the groundwork with Marchi granules, which indicates the terminal breaking up of the spino-thalamic fibres. On the other hand, the isolated degenerating fibres found in the medial part of the pars externa appear to be fibres of passage directed towards the lateral border of the nucleus. Further rostrally, in sections through the middle of the lateral geniculate body and in front of the level of the medial geniculate body, very few osmic-stained fibres are to be seen. However, there are a few very distinct degenerating fibres here along the ventral part of the lateral border of the pars externa of the ventral nucleus, and in the same area there is a scattered deposit of Marchi granules among the cells of the nucleus (Fig. 8 C). Tracing the sections forwards, an occasional degenerating fibre may be seen in the pars externa as far forwards as the level of the rostral extremity of the centre median nucleus. Here, however, they are extremely scattered, and only one or two can be identified in

each section. On the right side of the thalamus (the opposite side to the lesion) occasional degenerating fibres are seen limited to the same area as those on the left side.

Nowhere in the thalamus is there any Marchi staining in the pulvinar, lateral nucleus (elements *a* and *b*), pars arcuata of the ventral nucleus, centre median nucleus or dorso-medial nucleus.

Experiment G. O.M. 119. Operation 10 January 1936, killed 22 January 1936.

The object of this experiment was to interrupt as many of the ascending tract fibres as possible on one side immediately behind the caudal level of the thalamus. In this way the maximum extent of the terminal distribution in the thalamus of afferent fibres from the mid-brain, hind-brain and spinal cord (so far as they are shown by the Marchi technique) would be determined. A large osteoplastic flap was raised in the posterior parietal and occipital region of one side of the skull. The occipital pole of the hemisphere was mobilized by severing its venous connexions with the sagittal and transverse sinuses by means of the endothermy apparatus, and retracted upwards. The tentorium cerebelli was thus fully exposed. Working forwards along its upper surface, the splenium of the corpus callosum and the anterior colliculi were brought into view. A fine ophthalmic knife with a blunted tip was introduced in a vertical position close to the mid-line at the rostral border of the anterior colliculus, and pushed ventrally until it reached the base of the skull. The knife was then carried laterally in order to cut through the mid-brain transversely on one side at this level. Very little haemorrhage ensued and was quickly checked by slight pressure. The animal made a rapid recovery.

Histological examination of the lesion

Serial sections were made through the mid-brain and stained by the Marchi method. They show that dorsally the lesion penetrates through the caudal margin of the splenium and the rostral margin of the anterior colliculus close to the mid-line. It enters the mid-brain almost vertically, involving the most caudal fibres of the posterior commissure, and penetrating the central grey matter immediately to the right of the cerebral aqueduct (Fig. 9 A). Further down it cuts across the mesencephalic tract of the fifth nerve, and interrupts a considerable proportion of the central tegmental fasciculi (which here contain secondary trigeminal fibres). The central tegmental fasciculi are thickly strewn with degenerating fibres which can be traced up to the thalamus. The right brachium conjunctivum is cut through just caudal to its decussation, and its fibres, stained deeply with osmic acid, can be traced in continuity across the mid-line to the red nucleus of the left side. On the other hand, the red nucleus of the right side is free of osmic staining, the fibres of the left brachium conjunctivum having escaped injury. Further ventrally, the lesion cuts right across the fillet system as it is running dorso-laterally to enter the caudal pole of the thalamus. It appears from the sections that all the elements of the

fillet system are thus involved (Fig. 9 B). Finally, the lesion penetrates the substantia nigra of the right side and pierces the middle third of the cerebral peduncle to reach the basal surface of the mid-brain (Figs. 10 A, 10 B).

Course of degenerating fibres

On the right side there is profuse and conspicuous Marchi degeneration in the whole of the fillet system as it enters the thalamus, while the crossed brachium conjunctival fibres on this side are quite unstained.

On the left the opposite is the case, for here the fillet system is free of Marchi degeneration, while the crossed brachium conjunctivum fibres are heavily stained. The latter run up to the red nucleus of the left side, some of the fibres leaving the main bundle to reach the oculomotor nucleus of the left side by penetrating among the fasciculi of the medial longitudinal bundle.

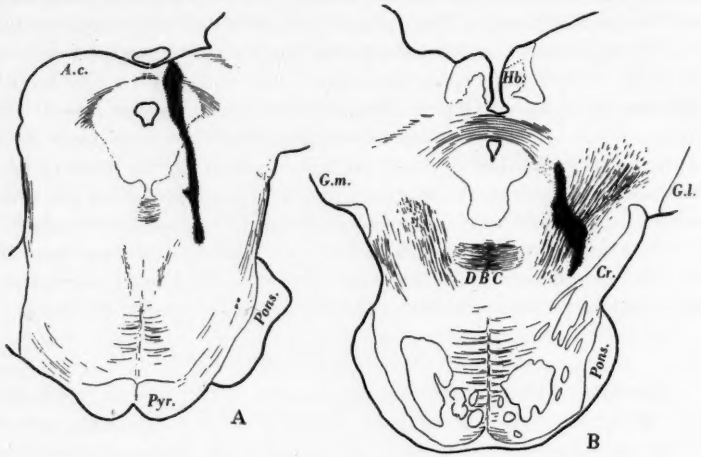


Fig. 9. The lesion in the mid-brain in experiment G (O.M. 119).

The oculomotor nucleus of the left side is strewn fairly thickly with Marchi granules. On the right side it is free of osmic deposit. In addition, degeneration is present in the tectospinal tract from the right anterior colliculus and can be followed through the dorsal tegmental decussation to the left side of the brain-stem. There are many degenerating fibres in the commissure of the anterior colliculus which extend into the colliculus of the left side, while a few scattered Marchi-stained fibres are also present in the posterior commissure. The course of degenerating fibres into the thalamus may most conveniently be dealt with separately on each side.

On the right side the fibres which reach the thalamus run in two main streams—in the fillet and in the central tegmental fasciculi, though where they enter the thalamus these two systems are not sharply separated from each

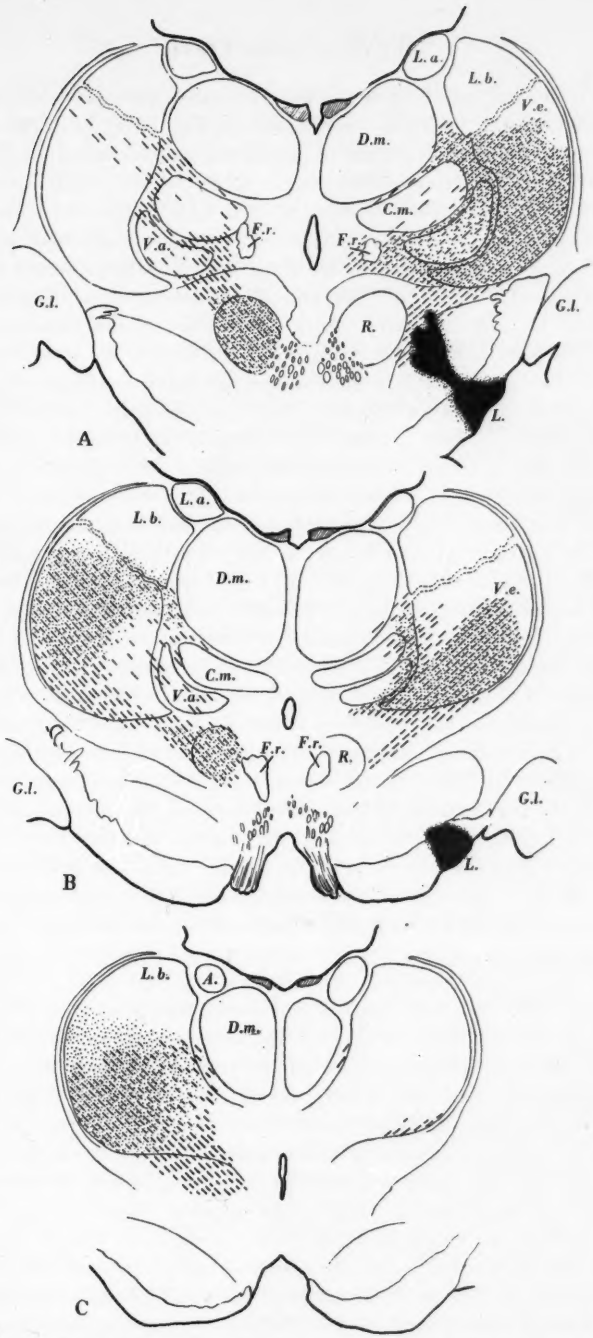


Fig. 10. The distribution of degenerating fibres in the thalamus in experiment G (O.M. 119).

other. The degenerating fibres of the fillet system course dorso-laterally from a position immediately lateral to the red nucleus (Fig. 10 A). The great majority of them form a conspicuous stream of interlacing osmic-stained fibres permeating the pars externa of the ventral nucleus at its posterior extremity. At this level the whole of this nuclear element is filled with degenerating fibres, while among these fibres the interstitial substance is sprinkled with Marchi granules. Towards the level of the rostral border of the centre median nucleus, the upper part of the pars externa of the ventral nucleus becomes clear of degenerating fibres (Fig. 10 B), and the latter, as the sections are traced forwards, rapidly disappear in a dorsi-ventral direction. When the level of the caudal margin of the anterior nucleus is reached, degenerating fibres have completely disappeared from the ventral nucleus, except for a very few which are still to be seen for a few sections at its extreme ventro-lateral margin (Fig. 10 C). The degenerating fibres in the pars externa of the ventral nucleus enter it mainly from the ventral medullary lamina. Some, however, run forwards and enter its medial aspect from the intermediate and medial medullary laminae. In the latter, a few can be followed as far rostrally as the transverse level of the anterior nucleus (Fig. 10 C), but these cannot be traced from the medial lamina into any of the adjacent thalamic nuclei. Possibly they end in the interstitial cells of the lamina (nucleus centralis lateralis of some authors).

The pars arcuata of the ventral nucleus is also filled with degenerating fibres throughout most of its extent, and on this side it is sprinkled with a deposit of Marchi granules, which, however, is not so dense as in the pars externa except at its dorso-lateral extremity. The fibres which permeate the arcuate nucleus are also very distinctly finer than those of the main part of the fillet which reach the pars externa of the ventral nucleus. The sections suggest that the degenerating fibres in the arcuate nucleus are derived from the medial fasciculi of the fillet system or from the central tegmental fasciculi, or both. Certainly the great majority of the lemniscal fibres skirt the lower margin of the arcuate nucleus and sweep round it to reach the pars externa of the ventral nucleus. It has been noted that the dorso-lateral extremity of the arcuate nucleus is more densely occupied by degenerating fibres. At the rostral end of the nucleus this is the only part which shows Marchi staining (Fig. 10 B).

The degenerating fibres in the central tegmental fasciculi run into and through the nucleus parafascicularis, and it seems probable that a proportion of them end here. Others turn antero-laterally at this level and appear to end in the arcuate nucleus. It is not possible, however, to be certain of this.

There is a complete absence of osmic-stained fibres in the substance of the dorso-medial nucleus, though a number may be followed forwards in the ventral part of the medial medullary lamina which forms a capsule for this nucleus. Further, no degenerating fibres are present in the elements of the lateral nucleus (*L. a.* or *L. b.*), in the nuclei of the pulvinar, in the medial and lateral geniculate bodies, or in the anterior nucleus. The centre median nucleus contains isolated Marchi-stained fibres which are running in a dorso-lateral

direction. They are more numerous near the posterior margin of the nucleus, but even here they are not very conspicuous. There is no sprinkling of osmic granules in the nucleus, which might indicate the breaking up of terminal fibres here, and the serial sections suggest strongly that the few degenerating fibres which are to be seen in the centre median nucleus are fibres of passage only.

On the left side, the Marchi degeneration is confined to the fibres of the brachium conjunctivum. The red nucleus of this side is filled with osmic deposit, and from its rostral aspect degenerating fibres are continued in an anterior and dorsi-lateral direction to reach the thalamus. At the caudal end of the thalamus these fibres enter it from the region of the medial part of the subthalamus, and at this level the ventral medullary lamina contains no degenerating fibres (Fig. 10 A). The brachium conjunctivum fibres can here be traced partly through the pars arcuata of the ventral nucleus, but mainly run in the intermediate and medial medullary laminae. From the latter, a few enter the most dorsal part of the pars externa of the ventral nucleus (Fig. 10 A). As the sections are traced forwards, degenerating fibres begin to enter the pars externa from below by way of the ventral medullary lamina, and, at the level of the rostral margin of the centre median nucleus, most of the pars externa (except for its ventro-medial part) shows Marchi degeneration (Fig. 10 B). Further forwards, at the level of the caudal margin of the anterior nucleus, these degenerating fibres are strewn throughout the ventral nucleus. As the sections are traced forwards from here, they become gradually restricted to the more ventro-lateral parts of the nucleus, and in this region a few Marchi-stained fibres may be seen close to the anterior extremity of the ventral nucleus.

As on the right side, there is no evidence of Marchi degeneration in the dorso-medial nucleus or in the elements of the lateral nucleus and pulvinar. A few degenerating fibres are to be seen in the arcuate nucleus and in the caudal part of the centre median nucleus, but it seems probable that these are fibres of passage only. The degenerating fibres on the left side are all of a finer calibre than those of the fillet system on the right side.

Experiment H. O.M. 122. Operation 17 January 1936, killed 29 January 1936.

In this animal a lesion was made involving both superior cerebellar peduncles. As in the previous experiment, the occipital lobe was exposed on one side by raising an osteoplastic flap, and was retracted upwards. The tentorium cerebelli was then incised so as to expose the superior vermis of the cerebellum. An ophthalmic knife was passed through the vermis and carried laterally on either side in order to sever the peduncles. The animal made a good recovery, but showed a characteristic cerebellar tremor and ataxia until its death.

Histological examination of the lesion

Serial Marchi sections were cut throughout the extent of the lesion. The latter was found to penetrate the superior vermis in the median plane, and to involve the brachia conjunctiva on both sides at the level where they emerge

from the cerebellar hemispheres. It also involves the roof nuclei. On the right side it reaches as far as the lateral margin of the fourth ventricle in its upper part, reaching here some of the fibres of the tegmental fasciculi which, as Wallenberg has shown, comprise a portion of the secondary trigeminal path, and extending partly into the vestibular nuclei. Further rostrally on this side the lesion reaches the rostral border of the brachium pontis, involving here also a portion of the lateral fillet system immediately in front of the pons. At this level spino-thalamic and spino-tectal fibres are running up among the fibres of the lateral fillet system, and some of these have been interrupted by the lesion. The lesion, therefore, was rather more extensive than had been intended. There is abundant Marchi degeneration in the medulla among fibres of the vestibulo-spinal tract, the posterior longitudinal bundle and the central tegmental fasciculi. In the following description, however, attention will be confined to the degenerating fibres which extend to the thalamus.

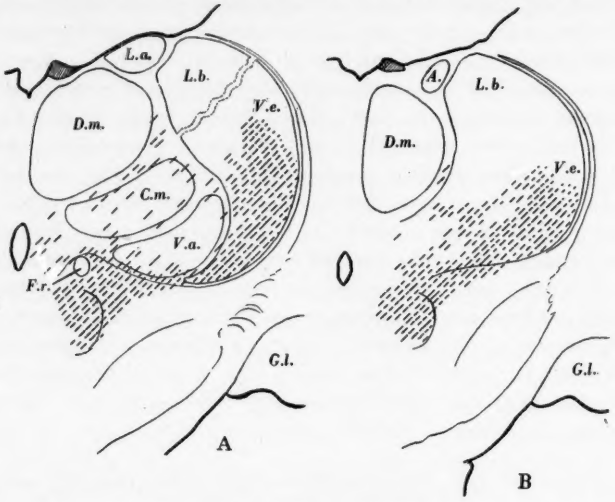


Fig. 11. The distribution of degenerating fibres in the thalamus in experiment H (O.M. 122).

Course of degenerating fibres

Immediately above the level of the lesion the fibres of both brachia conjunctiva are extensively stained with osmic acid. These degenerating fibres can be traced through the decussation of the brachia to the red nuclei of the opposite sides, whence many of them extend into the thalamus. Scattered degenerating fibres are also to be seen among the fibres of the lateral fillet. The subsequent course of the latter show them to belong to the spino-tectal and spino-thalamic tracts. At the level of anterior colliculi, scattered degenerating fibres are fairly numerous in the grey matter immediately surround-

ing the cerebral aqueduct, and quite a number of fibres in the central tegmental fasciculi of both sides also show Marchi staining. The origin of this latter degeneration is evidently the result of the fact that the lesion on the right side involved part of the secondary path of the trigeminal nerve which—as Wallenberg has shown in the rabbit—lies immediately under the brachium conjunctivum at the lateral margin of the 4th ventricle (see Fig. 10 of his paper, 1895). A few degenerating fibres extend into the anterior colliculus and across the commissure of the anterior colliculus to the opposite side. The medial longitudinal fasciculus, especially of the right side, is extensively degenerated, and from this numerous fibres extend into the nuclei of the third and fourth cranial nerves. The degenerating spino-thalamic fibres can be traced up in a position immediately deep to the inferior brachium. From here they pass medial to the medial geniculate body through the region of the nucleus limitans, where they splay out in a lateral and dorsal direction to enter the caudal extremity of the pars externa of the ventral nucleus.

On the right side, the degenerating fibres which enter the thalamus run in the spino-thalamic tract, the central tegmental fasciculi and the brachium conjunctivum. As they reach the thalamus these systems are distinct, but they rapidly come into such close relation with each other that their subsequent course in the thalamus cannot be followed separately. The more dorsal fibres run through the region of the parafascicular nucleus and many of them through the capsule of the centre median nucleus. Scattered degenerating fibres penetrate the substance of the centre median nucleus, especially in its caudal part, but there is no certain evidence that they end here. This nucleus contains no Marchi deposit among its cells which might indicate the breaking up of fibres of termination. Above and in front of the centre median nucleus, these degenerating fibres are seen to enter the medial medullary lamina in which they can be traced forwards as far as the transverse level of the anterior nucleus of the thalamus. The ventral medullary lamina contains numerous degenerating fibres at caudal levels of the thalamus, which in general course dorsally and laterally to enter the pars externa of the ventral nucleus. This nuclear element is almost completely filled with Marchi-stained fibres in its caudal part, though not so densely as in cases of lesions involving the medial fillet system (Fig. 11 A). In front of the level of the centre median nucleus, degenerating fibres can only be found in the lower part of the ventral nucleus (Fig. 11 B). They can be traced in this position as far forwards as the level of the middle of the anterior nucleus, beyond which they are no more evident. Comparison with previous experiments in which the tracts were separately involved indicates that the degenerating fibres in the caudal part of the pars externa of the ventral nucleus are derived from the spino-thalamic system, while those more rostrally are fibres of the brachium conjunctivum. The latter, however, are not so extensive anteriorly as on the left side of the thalamus or in experiment G, possibly because the left brachium conjunctivum was in the present case not completely involved. Most of the degenerating fibres which

enter the pars externa of the ventral nucleus from the ventral medullary lamina skirt the lower margin of the pars arcuata. Isolated fibres showing Marchi staining do penetrate the nucleus, however, and run through its medullary capsule. These seem mainly to be derived from the brachium conjunctivum. The sections suggest that these few fibres do not end in the arcuate nucleus, but are fibres of passage merely. Further medially, a number of degenerating fibres are to be seen in the periventricular grey matter on the medial aspect of the fasciculus retroflexus and close to the ventricle (Fig. 11 A).

On the left side of the thalamus the distribution of degenerating fibres is practically identical with that of the left side of the thalamus in experiment G, in which degeneration was confined to the brachium conjunctivum.

DISCUSSION OF RESULTS

In discussing the results of the experiments which have been recorded in this paper, it is convenient first to consider separately the various afferent fibre systems which have been involved by the lesions.

The termination of the medial fillet

As is well known, the fibres of the medial fillet take origin in the cuneate and gracile nuclei in the medulla. In the first two experiments localized lesions were produced in the gracile and cuneate nuclei respectively, while in experiments C and D the fillet fibres were interrupted in part soon after their origin from these nuclei. The Marchi degeneration following these lesions indicates that the medial fillet probably ends entirely in the pars externa of the ventral nucleus, reaching in its extent as far forwards as approximately the level of the rostral border of the centre median nucleus. The majority of the fibres enter the ventral nucleus from below by way of the ventral medullary lamina of the thalamus. Some, however, especially those from the cuneate nucleus, penetrate the caudal extremities of the centre median nucleus and the arcuate nucleus and, running in the intermediate and the ventral part of the medial medullary lamina, pass into the pars externa of the ventral nucleus from its medial aspect. No sure evidence was found of the actual termination of medial fillet fibres in the pars arcuata of the ventral nucleus or in the centre median nucleus, the scattered degenerating fibres found in the posterior ends of these elements being probably fibres of passage only. In all the experiments the lateral nucleus (both elements *a* and *b*) was quite free of Marchi degeneration. In many sections the contrast between the osmic-filled ventral nucleus and the clear groundwork of the lateral nucleus along their line of junction is very striking. The contrast is sufficiently abrupt to permit considerable assurance in the statement that no medial fillet fibres end in the lateral nucleus of the thalamus. It has been shown experimentally that the pars externa of the ventral nucleus, but not the lateral nucleus, projects on to the area postcentralis of the cortex (5). It may be inferred, therefore, on the basis of experi-

ments recorded here, that the afferent impulses conveyed by the medial fillet must be projected on to this area. With regard to the topographical relation in the ventral nucleus of terminal fibres conveying impulses from different levels of the body, these experiments indicate that those from lower levels reach the more lateral parts of the ventral nucleus, and those from higher levels the more medial parts. Thus, in experiment A the nucleus gracilis was injured, and it is known that this nucleus receives the fibres of Goll's tract which conveys impulses from the lower half of the trunk and the lower extremity. In this case, the degenerating fibres were concentrated along the ventro-lateral margin of the pars externa. In experiment B the lesion involved the cuneate nucleus which receives impulses by way of Burdach's column from the upper half of the trunk and the upper extremity, and here the degenerating fibres end predominantly in the central portion of the pars externa of the ventral nucleus, the lateral part remaining free of Marchi staining (Fig. 3 B). These conclusions confirm the impression gained by Wallenberg (20) from his observations on lower mammals that, in general, a more caudal origin of afferent impulses corresponds to a more latero-ventral position in the thalamus. They also fall into line with recent experiments which have demonstrated that the more lateral part of the pars externa of the ventral nucleus projects on to the upper end of the post central gyrus, while the more medial part projects on to the lower end (5, 16). While the Marchi technique does not permit of a very precise definition of the several areas of termination in the ventral nucleus of different groups of fillet fibres, the study of cell atrophy following cortical ablations in the experiments just quoted suggests that there is probably quite a sharply defined topographical representation in this nucleus of different sensory regions of the body.

The observation that medial fillet fibres terminate probably exclusively in the pars externa of the ventral nucleus in the monkey is in accord with the results of previous studies. In 1895 Mott (12) made an experimental enquiry on the afferent tracts of the central nervous system of the monkey. Although he did not concern himself with a detailed study of their thalamic termination, his figures indicate that in experiments in which the gracile and cuneate nuclei were destroyed, degenerating fibres all ended in the pars externa of the ventral nucleus. Vogt (15) found that fibres from the cuneate nucleus pass to the caudal end of this nuclear element, and though some of the more medially situated fibres were also seen to enter the capsule of the centre median nucleus and to penetrate the arcuate nucleus, it is probable that they all eventually terminated in the pars externa. Wallenberg (20) found in the rabbit that degenerating fibres following lesions in the posterior column nuclei extend into a region of the ventral nucleus of the thalamus, which, from his descriptions and figures, evidently corresponds to the pars externa of the macaque thalamus. Similar observations were made by Probst (13) in 1900. Recently Ranson & Ingram (14) defined very clearly the precise termination of the medial fillet in the cat, and demonstrated that it ends in the greater part of the pars externa of the

ventral nucleus except for its rostral end. Observations on the rat (3) similarly show the relation of the medial fillet to the pars externa of the ventral nucleus.

It is worth while emphasizing the fact that the experiments recorded in this paper show that the terminal fibres of the medial fillet in the thalamus are distributed over precisely that part of the ventral nucleus whose cells undergo complete atrophy after lesions confined to the postcentral gyrus (area post-centralis).

Spino-thalamic tracts

In two experiments (E and F) a hemisection of the spinal cord was made in order to interrupt on one side the spino-thalamic tracts. In one case the lesion was in the cervical region, between the fourth and fifth cervical nerve roots, and, in the other, in the thoracic region between the third and fourth thoracic nerve roots. These cases show that proportionately many more degenerating spino-thalamic fibres follow the cervical lesion. This corroborates the statement of Collier & Buzzard on human material that "the number of spino-tectal and spino-thalamic fibres was considerably greater in lesions of the cervical enlargement than in lesions at lower levels". In the rabbit, according to Wallenberg (20), spino-thalamic fibres take origin only from the cervical part of the spinal cord.

The spino-thalamic tract occupies quite a lateral position in the mid-brain, and its fibres run in a dorsal direction to form a component of the lateral fillet system. They approach the thalamus from a position immediately medial to the medial geniculate body (Fig. 8 A), extending from here dorso-medially to the nucleus parafascicularis. There is evidence from the two experiments that the fibres arising from more caudal levels occupy a more lateral position at their entry into the thalamus. In the cervical lesion many penetrated the parafascicular nucleus (which in this case was richly strewn with osmic granules), while in the thoracic lesion the degenerating fibres were concentrated close to the medial aspect of the medial geniculate body. In the thalamus at least the great majority of spino-thalamic fibres end in the pars externa of the ventral nucleus, the site of their termination corresponding closely with that of the medial fillet fibres. Those taking origin from the lower levels of the cord enter the ventral nucleus from below by way of the ventral medullary lamina, while those from higher levels mainly penetrate the nucleus from its medial aspect, approaching it by way of the intermediate medullary lamina and the ventral part of the medial medullary lamina. As in the case of the medial fillet, some of the latter fibres pass through the caudal extremities of the centre median and arcuate nuclei, but the evidence of the sections suggests that they do not end in these elements. Within the pars externa of the ventral nucleus the distribution of degenerating fibres suggests that those of a more caudal origin terminate in a more lateral position. The question arises whether the spino-thalamic fibres reach any other thalamic nuclei. It has already been noted that the few scattered fibres in the centre median and arcuate nuclei are probably fibres of passage only. No degenerating fibres were found in these

experiments (or in experiment G in which the whole fillet system was involved at its entry into the thalamus) in the dorso-medial nucleus, or in the lateral nucleus (except possibly for its extreme ventral border). In experiment E, and in experiment H in which the spino-thalamic tract was involved, a few degenerating fibres were found in the periventricular grey matter medial to the fasciculus retroflexus at the caudal end of the thalamus (Fig. 7 A), but they were absent from this region in experiment F. In experiment E, also (and in experiment G), the medial medullary lamina contained many Marchi-stained fibres, and it seems probable that some end in the nuclei of this lamina (nucleus paracentralis and nucleus centralis lateralis) since they could be traced forwards beyond the level at which they are found in the neighbouring region of the pars externa of the ventral nucleus (Figs. 7 C and 10 C). However, the Marchi technique is not adequate to decide this point, though it may be remarked that ablation experiments on the cortex indicate that neither the nuclei of the medial medullary lamina or the periventricular grey matter are connected to the cortex (17). Following lesions in the spinal cord of the monkey, Mott (12) followed ascending fibres by the Marchi method and found "a few *apparently* going on with the fibres of the fillet to the optic thalamus". His figure shows these fibres ending in what appears to be the medial part of the caudal extremity of the pars externa of the ventral nucleus, but the diagram is too crude to allow of any certainty on this point. In human material Collier & Buzzard (6) traced the spino-thalamic tract up to a point where it came "in contact with the mesial surface of the internal geniculate body", after which "it swung abruptly outwards—into the ventral nucleus of the thalamus". The fact that spino-thalamic fibres end preponderatingly in the same thalamic nucleus which receives the termination of the medial fillet fibres is worth emphasizing because of the generally accepted thesis that these two tracts serve to convey afferent impulses of different categories.

Dentato-thalamic fibres

It is well known that a considerable proportion of the efferent cerebellar fibres in the brachium conjunctivum pass by the opposite red nucleus and continue their way on to the thalamus. Their destination in the thalamus in the monkey has been studied experimentally by Vogt (15), who found that they terminated in the "intermediate ventral nucleus", dorsal and rostral to the ending of the medial fillet. It may be noted that the "intermediate ventral nucleus" of Vogt's terminology corresponds to the rostral part of the pars externa of the ventral nucleus. In the cat, Ranson & Ingram (14) traced brachium conjunctivum fibres into the rostral pole of the pars externa of the ventral nucleus, and also into the arcuate nucleus. In two experiments (G and H) recorded in this paper, a lesion had been made in the superior cerebellar peduncle. The distribution of Marchi degeneration subsequently showed that its thalamic fibres end almost entirely in the dorsal and rostral parts of the pars externa of the ventral nucleus from about the level of the

middle of the centre median nucleus as far forwards as the level of the anterior nucleus. This area of termination corresponds in a very striking way to the area of complete cell atrophy which follows cortical lesions involving the precentral gyrus. Whether there is any overlapping in the ventral nucleus of the areas of termination of the fillet fibres and the brachial fibres cannot, of course, be decided by the Marchi technique, but a comparison of the sections gives the impression that this is not so. Contrary to the findings of Ranson & Ingram, no certain evidence was found of the termination of cerebellar fibres in the pars arcuata of the ventral nucleus. In this nucleus (as well as in the centre median nucleus) only isolated fibres of passage were found at their caudal extremities. This discrepancy is due to the fact that the arcuate nucleus as described in the cat is evidently not entirely homologous with the arcuate nucleus of the macaque thalamus. A comparison of relevant figures shows that probably only the caudal end of the cat's arcuate nucleus is the equivalent of the macaque arcuate nucleus, and this region seems to have been comparatively free of Marchi degeneration in the experiment of Ranson & Ingram. On the other hand, the rostral part of the cat's arcuate nucleus as figured by these authors occupies the position of the rostral part of the pars externa of the ventral nucleus in the monkey.

Trigeminal fillet

In two experiments (B and C) local lesions were produced on one side in the spinal nucleus of the fifth cranial nerve. In experiment B the lesion was uncomplicated by injury to other elements on the same side. The sections of this case indicate that very few fibres from the spinal nucleus reach the thalamus. Scattered degenerating fibres were found in the medial fillet and in the central tegmental fasciculi of the opposite side, and some of these could be traced into the medio-ventral extremity of the pars externa of the ventral nucleus. In experiment C, injury to the spinal nucleus of the fifth nerve was also followed by some Marchi degeneration in the central tegmental fasciculi of the opposite side, but the termination of these fibres in the thalamus could not be determined because of their mingling with medial fillet fibres which were also involved in this case. In experiment D, the position of the secondary trigeminal path in the central tegmental fasciculi was involved by a lesion, and degenerating fibres could be followed into the medial border of the pars externa of the ventral nucleus, entering it from the region of the parafascicular nucleus. The dorsal path of secondary trigeminal fibres was also affected by the lesion in experiment H, but in this case Marchi degeneration of these fibres was obscured by the injury to the brachium conjunctivum. These experiments serve to indicate that trigeminal fibres arising in the spinal nucleus end in the medio-ventral part of the pars externa of the ventral nucleus. Some may end in the parafascicular nucleus and the nuclei of the medial medullary lamina through which they course, but there is no evidence that any terminate in the centre median, arcuate or dorso-medial nuclei.

Although the attempt was made, unfortunately in no case was a lesion placed in the main or medullary sensory nucleus of the fifth nerve. Thus no positive evidence has been obtained as to the thalamic termination of secondary fibres from this important element. On the analogy of the medial and spinal fillets, it might be supposed that the thalamic fibres of all parts of the trigeminal nucleus probably end in the same region, i.e. in the medio-ventral portion of the pars externa of the ventral nucleus. Another possibility, however, is the pars arcuata of the ventral nucleus which is known to project, at least in part, on to the face area of the pre- or post-central gyrus.[1] In only one experiment of this series was there definite evidence of the termination of degenerating fibres in the arcuate nucleus, and that is experiment G. In this experiment the lesion must have involved secondary trigeminal fibres from the main sensory nucleus, but, since it also cut across many other fibre systems at the caudal boundary of the thalamus, no certain conclusions can be drawn from such an observation. Wallenberg's Fig. 5 C, 6 E (20), and Fig. 5 (19), seem to show quite clearly that in the rabbit secondary trigeminal fibres end largely in the pars externa of the ventral nucleus, while that portion of the ventral nucleus which is apparently the equivalent of the macaque arcuate nucleus is left quite clear of Marchi degeneration in his experiments.

General relation of thalamic nuclei to ascending tracts

It is clear that at least the great majority of the fibres of the medial and spinal lemnisci and of the brachium conjunctivum, which reach the thalamus, end in the pars externa of the ventral nucleus, the first two ending in that region of the nucleus which projects on to the area post-centralis, and the last in the more dorso-rostral part which projects on to the motor cortex. The Marchi technique does not allow a decision whether any of these fibres end in the intra-laminar nuclei through which they run to their main destination, e.g. the parafascicular nucleus and the nuclei of the medial medullary lamina, but in the case of spino-thalamic fibres there is some positive evidence that this is so.

There is no evidence that the pars arcuata of the ventral nucleus receives terminal fibres of the medial and spinal fillets or of the brachium conjunctivum. That it receives some afferent fibres is indicated by experiment G, in which a large lesion involved ascending paths immediately behind their entry into the caudal end of the thalamus, but the source of these fibres is uncertain.

There is no evidence that the centre median nucleus receives any terminal fibres from more caudal levels of the brain stem. In several of the experiments

[1] My own experiments, some of which await publication, show that the arcuate nucleus projects on to the precentral gyrus. It was assumed, on the basis of Brodmann's charts, that it connects with the true motor cortex. However, it has been shown by Bucy (*J. comp. Neurol.* vol. LXII, 1935) that in the macaque monkey the sensory cortex of the area postcentralis extends across the lower end of the central sulcus and occupies the lower end of the precentral gyrus. It is possible, therefore, that the arcuate nucleus is related to this forward extension of the sensory cortex rather than to the lower extremity of the motor cortex.

isolated degenerating fibres were found penetrating its caudal extremity, but they appear to be fibres of passage only.

In no case could degenerating fibres be traced into the substance of the lateral or dorso-medial nuclei. The experiments indicate that these nuclei receive no contribution from any part of the fillet system or from the cerebellum. The same observation applies to the elements of the pulvinar and the anterior nucleus.

As regards nuclei of the mid-line, in only two cases in which spino-thalamic fibres had been involved by the lesion were isolated degenerating fibres found in the periventricular grey matter at the most caudal extremity of the thalamus.

The cost of the animals used in this research was met by a grant from the Royal Society, which I wish gratefully to acknowledge.

ABBREVIATIONS

A.	Anterior nucleus.	*m.V*	Motor nucleus of fifth nerve.
A.c.	Anterior colliculus.	*N.c.*	Nucleus cuneatus.
C.m.	Centre median nucleus.	*N.c.e.*	Nucleus cuneatus externus.
Cr.	Crus cerebri.	*N.g.*	Nucleus gracilis.
D.m.	Nucleus dorso-medialis.	*N.l.*	Nucleus limitans.
F.	Fornix.	*P.*	Pulvinar.
F.r.	Fasciculus retroflexus.		
F.sol.	Fasciculus solitarius.	*Pr.*	Pretectal nucleus.
G.l.	Lateral geniculate body.	*Pyr.*	Pyramid.
G.m.	Medial geniculate body.	*R.*	Red nucleus.
Hb.	Habenular ganglion.	*R.b.*	Restiform body.
L.	Lesion.	*S.V*	Sensory nucleus of fifth nerve.
L. a.	Element of lateral nucleus.	*Sp.V*	Spinal nucleus of fifth nerve.
L. b.	„ „ „	*V.a.*	Pars arcuata of ventral nucleus.
Lem.	Medial lemniscus.	*V.e.*	Pars externa of ventral nucleus.
M.	Mammillo-thalamic tract.	*V.a.m.*	Pars antero-medialis of ventral nucleus.
M.m.	Medial mammillary nucleus.		

REFERENCES

(1) Aronson, L. R. & Papez, J. W. (1934). *Arch. Neurol. Psychopath.* vol. xxxii, p. 27.
(2) Cajal, S. R. Y. (1903). *Int. Congr. Med.*, Madrid, vol. Général, xiv, p. 277.
(3) Clark, W. E. Le Gros (1932). *Philos. Trans.* B, vol. ccxxii, p. 11.
(4) Clark, W. E. Le Gros (1936). *J. Anat.*, Lond., vol. lxx, p. 447.
(5) Clark, W. E. Le Gros & Boggon, R. H. (1935). *Philos. Trans.* B, vol. ccxxiv, p. 313.
(6) Collier, J. & Buzzard, E. F. (1903). *Brain*, vol. xxvi, p. 559.
(7) Crouch, R. L. (1934). *J. comp. Neurol.* vol. lix, p. 451.
(8) Elliot Smith, G. (1901). *J. Anat. Phys.* vol. xxxv, p. 431.
(9) Elliot Smith, G. (1910). *Lancet*, vol. i, p. 1.
(10) Friedemann, M. (1911–12). *J. Psychol. Neurol.* Bd. xviii, S. 309.
(11) Grünthal, E. (1934). *J. Psychol. Neurol.* Bd. xlvi, S. 41.
(12) Mott, F. W. (1895). *Brain*, vol. xviii, p. 1.
(13) Probst, M. (1900). *Arch. f. Psych.* Bd. xxxiii, S. 1.
(14) Ranson, S. W. & Ingram, W. R. (1932). *J. comp. Neurol.* vol. lvi, p. 257.
(15) Vogt, C. (1909). *J. Psychol. Neurol.* Bd. xii, S. 74.
(16) Walker, A. E. (1934). *J. comp. Neurol.* vol. lx, p. 161.
(17) Walker, A. E. (1935). *J. comp. Neurol.* vol. lxii, p. 407.
(18) Walker, A. E. (1936). *J. comp. Neurol.* vol. lxiv, p. 1.
(19) Wallenberg, A. (1895). *Anat. Anz.* Bd. xii, S. 95, 474.
(20) Wallenberg, A. (1900). *Anat. Anz.* Bd. xviii, S. 81.

LE NÉOPALLIUM DU MOUTON—ÉTUDE DE SON DÉVELOPPEMENT ET INTERPRÉTATION DE SES PLISSEMENTS

PAR R. ANTHONY
Professeur au Muséum national d'Histoire naturelle, Paris

ET J. DE GRZYBOWSKI
Professeur agrégé de l'Université de Varsovie

CE travail fait suite à nos publications antérieures sur le néopallium du Cheval,[1] du Porc[2] et du Bœuf.[3] L'ensemble de toutes ces recherches doit aboutir à une synthèse du cerveau des Ongulés dont nous avons déjà donné un premier aperçu[4] anticipant sur les conclusions que nous exposons ici relativement au cerveau du Mouton.

De même que dans nos publications précédentes, nous avons augmenté notre étude du développement du néopallium de quelques indications sur le développement du rhinencéphale.

En nous basant sur l'état du développement des très nombreux cerveaux de fœtus de Mouton que nous avons eu à notre disposition et qui proviennent tous des abattoirs de Paris, nous avons pu établir 9 stades dont le dernier correspond à un animal très proche de la naissance, son cerveau étant extrêmement voisin de celui d'un adulte. Nous avons fait notre possible pour que ces différents stades correspondent en gros à ceux que nous avons distingués chez le Bœuf.

Pour l'établissement de ces stades, la taille de l'animal n'a pas été prise en considération, car, ici, comme partout ailleurs, elle est loin de correspondre à l'état de développement du cerveau.

Stade	Longueur du télencéphale en mill.	Hauteur du télencéphale en mill.
I	9	7
I bis	10	8
II	15	12
III	17	14
III bis	20	15
IV	22	16
V	18	14
VI	26	19
VII	25	18
VIII	31	21
VIII bis	33	21
IX	42	24

[1] R. Anthony & J. de Grzybowski: "Le néopallium des Équidés. Étude du développement de ses plissements." *J. Anat.*, Lond., vol. LXIV, Jan. 1930.

[2] R. Anthony & J. de Grzybowski: "Le néopallium des Suidés. Étude de son développement et interprétation de ses plissements. *Arch. Zool. exp. gén.*, vol. jubilaire, t. LXXIV, 1931.

[3] R. Anthony & J. de Grzybowski: "Le néopallium du Bœuf. Étude de son développement et interprétation de ses plissements." *J. Anat.*, Lond., vol. LXVIII, July 1934.

[4] R. Anthony & J. de Grzybowski: "L'operculisation du territoire central du néopallium chez les Ongulés." *Neurolog. Bladen* (*Festbunden Prof. C. U. Ariens Kappers*), 1934.

Stade I

Ce stade I est absolument identique au stade I du Bœuf.

Sur la face externe (Fig. 1), on voit seulement la rhinale antérieure, complète avec un début antérieur de rhinale postérieure; le néopallium est complètement lisse.

Le rhinencéphale ne possède pour encore que l'endorhinale toujours, par conséquent, d'un développement très précoce.

La précocité de développement de la rhinale antérieure par rapport à la postérieure et le développement d'avant en arrière de cette dernière (Porc, Bœuf, Carnassiers, Primates) (I) s'éffirment une fois de plus comme des caractères très généraux.

Sur la face interne (Fig. 2), on ne voit que la fissure hippocampienne est déjà bien développée dans ses régions postérieures (fornicienne) et moyenne (supracalleuse). La *fissura prima* de His qui entaille déjà chez le Bœuf le bord inférieur du lobe antérieur du rhinencéphale n'est pas encore indiquée ici.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 77{\cdot}7.$$

Stade I bis

La seule différence que présente le stade I bis par rapport au stade I consiste dans le complet développement de la rhinale postérieure (Fig. 3), au moins sur la face externe

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 80{\cdot}0.$$

Stade II

En ce qui concerne la face externe (Fig. 4), bien que l'état de développement soit sensiblement le même que chez le Bœuf, une différence morphologique capitale est à signaler: le creusement de la fosse sylvienne débute chez le Bœuf par le creusement de l'*ectosylvia* antérieure; ici, c'est à dire chez le Mouton, il débute par le creusement de l'*ectosylvia* postérieure.

[1] Le Cheval fait probablement exception à cette règle. Voir R. Anthony & J. de Grzybowski, *loc. cit.* 1930.

Légendes des figures 1–10

Fig. 1. Stade I. Face latérale externe gauche.
Fig. 2. Stade I. Face latérale interne droite.
Fig. 3. Stade I bis. Face latérale externe gauche.
Fig. 4. Stade II. Face latérale externe gauche.
Fig. 5. Stade II. Face latérale interne gauche.
Fig. 6. Stade III. Face latérale externe droite.
Fig. 7. Stade III. Face supérieure.
Fig. 8. Stade III. Face latérale interne gauche.
Fig. 9. Stade III bis. Face latérale externe droite.
Fig. 10. Stade III bis. Face supérieure.

Fig. 1.

Fig. 2.

Fig. 3.

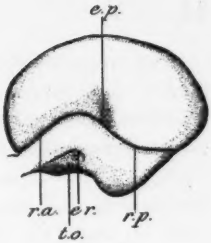


Fig. 4.

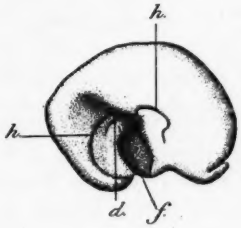


Fig. 5.

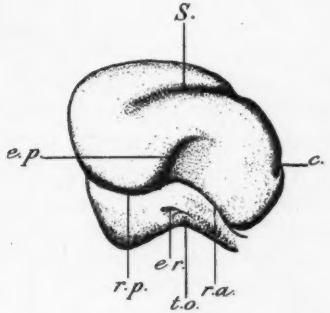


Fig. 6.

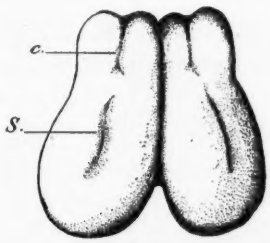


Fig. 7.

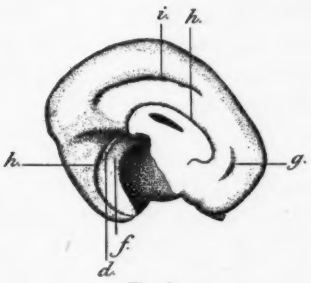


Fig. 8.

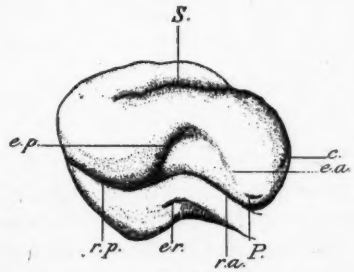


Fig. 9.

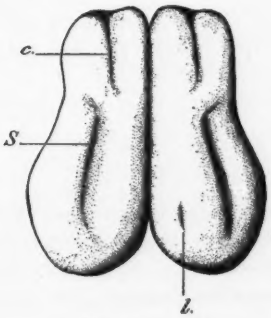


Fig. 10.

Par rapport à ce qu'on constate chez le Bœuf, la face interne (Fig. 5) est d'un développement un peu plus avancé que l'externe, en ce sens qu'il y existe un début supérieur de *sulcus fimbrio-dentatus*, c'est à dire un début de séparation extérieurement visible entre le *fimbria* et le *gyrus dentatus*. C'est également dans sa partie supérieure que se creuse au début, chez le Bœuf, le *sulcus fimbrio-dentatus*; mais ce creusement ne se produit chez lui beaucoup plus tard, au stade IV, c'est à dire à un moment où les plissements néopalléaux externes sont beaucoup plus développés et plus nombreux.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 80{\cdot}0.$$

Stade III

Ce stade correspond à peu près au stade IV du Bœuf. Sur la face externe (Fig. 6 et 7), on constate: la non-indication d'*ectosylvia* antérieure dont il convient de relever par conséquent le développement tardif chez le Mouton; le développement déjà avancé de la *suprasylvia* (à l'apparition de laquelle nous n'avons pas assisté) et du coronal qui entaille déjà le bord marginal antérieur de l'hémisphère, alors qu'il n'en n'est point ainsi chez le Bœuf. La *presylvia* et le latéral n'ont point encore fait leur apparition; et il en est de même du *sulcus sagittalis*, sur le lobe piriforme du rhinencéphale, qu'on voit déjà exister au stade IV du Bœuf.

La face interne (Fig. 8) est exactement dans le même état de développement qu'au stade IV chez le Bœuf [apparition de l'intercalaire (partie moyenne) et du *genualis*].

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 82{\cdot}3.$$

Stade III bis

Le stade III bis dont nous aurions pu faire un stade autonome est caractérisé par l'apparition sur la face externe (Fig. 9 et 10) de l'*ectosylvia* antérieure, de la *presylvia* et du latéral (à droite seulement). Il n'existe pas de *sulcus sagittalis* au rhinencéphale. La face interne (Fig. 11) est restée semblable à ce qu'elle était au stade précédent.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 75{\cdot}0.$$

Stade IV

Le stade IV est marqué sur la face externe (Fig. 12 et 13) par l'apparition du latéral gauche et surtout par l'élargissement et l'abaissement de la courbe ectosylvienne, ce qui est en rapport avec l'allongement antéro-postérieur plus marqué du télencéphale; le *sulcus sagittalis* ne s'est pas encore montré au rhinencéphale.

La face interne (Fig. 14) est caractérisée: par l'allongement et par l'apparition, au bord marginal postérieur, de la rhinale postérieure qui entaille ce bord d'une profonde encoche; par l'apparition d'une ébauche postérieure du calloso-marginal; par le creusement et l'allongement de l'intercalaire; enfin, au rhinencéphale, par l'allongement du sulcus *fimbrio-dentatus*.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 72{\cdot}7.$$

Stade V

Le stade V est marqué, sur la face externe (Fig. 15), par l'apparition d'un sillon que, dans le cerveau du Bœuf, nous avons désigné par la lettre γ. Mais, alors que, dans le cerveau du Bœuf, ce sillon que nous avons considéré comme une dépendance de la *suprasylvia* antérieure est indépendant de l'*ectosylvia*, il commence, ici, en connexion avec l'*ectosylvia* antérieure: les stades suivants nous montreront d'ailleurs qu'il est bien des cas, chez le Mouton, où les relations entre γ et l'*ectosylvia* n'existent pas. De plus, on voit aussi une liaison s'établir entre la *suprasylvia* et le coronal. Enfin, au rhinencéphale, le *sulcus sagittalis* a commencé de se montrer; son apparition est donc très tardive.

Sur la face interne (Fig. 16), il est à noter qu'on ne voit pas, comme au stade précédent, de début de calloso-marginal; de même, la rhinale postérieure n'entame pas le bord postérieur de l'hémisphère; par contre, le sulcus *fimbrio-dentatus*, a acquis sa longueur normale et définitive

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 77{\cdot}7.$$

Stade VI

Au stade VI, le sillon γ n'existe pas sur la face externe (Fig. 17), comme au stade précédent; par contre, on voit apparaître le sillon que nous avons désigné par la lettre δ chez le Bœuf et que nous avons interprété comme étant le sillon oblique de Holl et d'Elliot Smith. De plus, l'*ectosylvia* présente, en son point de coudure, un sillon vertical (sillon axial de la 2ème circonvolution arquée); c'est un début de constitution du complexe sylvien.

Sur la face interne (Fig. 18) il n'y a rien de particulier, à signaler, si ce n'est, comme au stade précédent, l'absence de début de calloso-marginal.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 73{\cdot}0.$$

Stade VII

Le stade VII est caractérisé par une complication déjà beaucoup plus accusée.

Face externe (Fig. 19 et 20): Complication de la lèvre inférieure de la 2ème circonvolution arquée, en avant (*ectosylvia* antérieure); allongement des sillons γ et δ (γ ne communiquant pas avec l'*ectosylvia* antérieure); allongement du sillon vertical surmontant le sommet de l'*ectosylvia*, par conséquent dé-

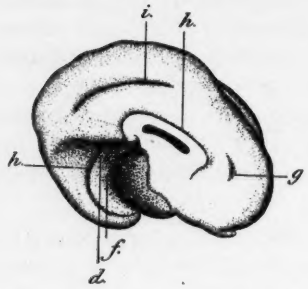


Fig. 11. Stade III bis. Face latérale interne gauche.

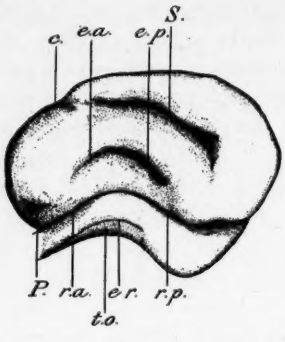


Fig. 12. Stade IV. Face latérale externe gauche.

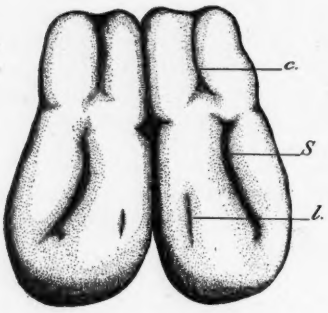


Fig. 13. Stade IV. Face supérieure.

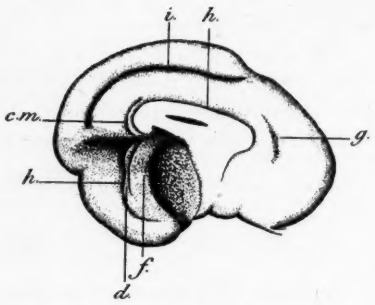


Fig. 14. Stade IV. Face latérale interne gauche.

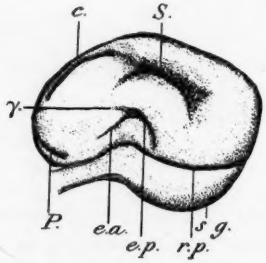


Fig. 15. Stade V. Face latérale externe gauche.

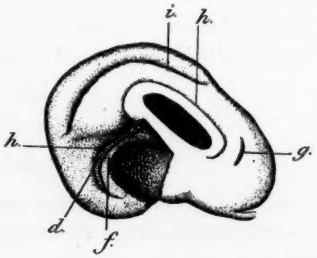


Fig. 16. Stade V. Face latérale interne gauche.

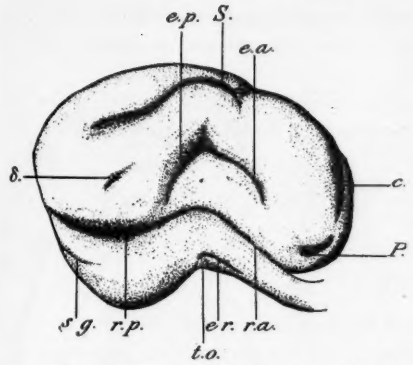


Fig. 17. Stade VI. Face latérale externe droite.

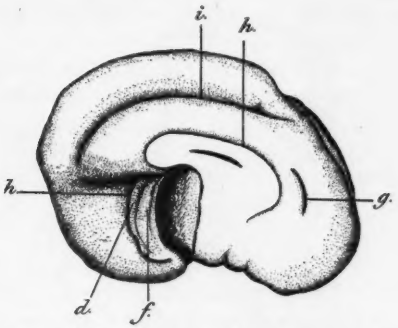


Fig. 18. Stade VI. Face latérale interne gauche.

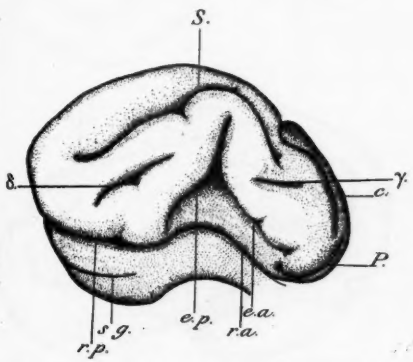


Fig. 19. Stade VII. Face latérale externe droite.

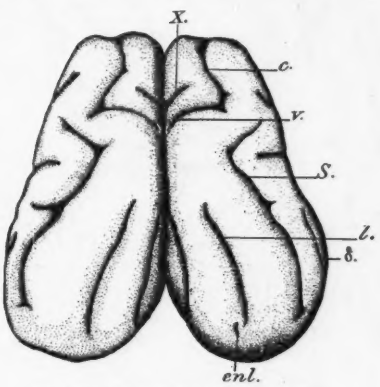


Fig. 20. Stade VII. Face supérieure.

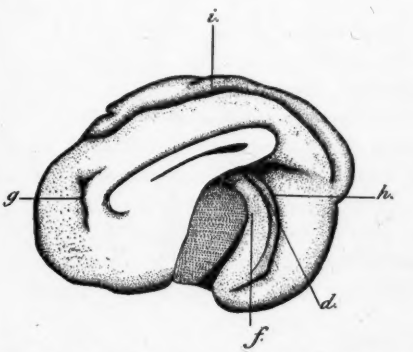


Fig. 21. Stade VII. Face latérale interne droite.

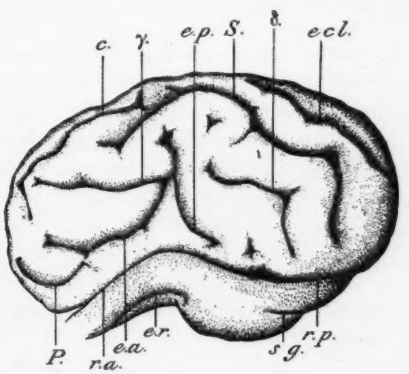


Fig. 22. Stade VIII. Face latérale externe gauche.

veloppement plus avancé du complexe sylvien; apparition du vertical; apparition du crucial en continuation de l'intercalaire; apparition, à droite, de l'entolatéral.

Face interne (Fig. 21): Comme dans le stade précédent, avec cette seule différence que l'intercalaire se prolonge en avant et donne le crucial sur la face externe

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 72{\cdot}0.$$

Stade VIII

Les particularités du cerveau au stade VIII sont les suivantes:

Face externe (Fig. 22 et 23): La *presylvia* qui est complètement developpée

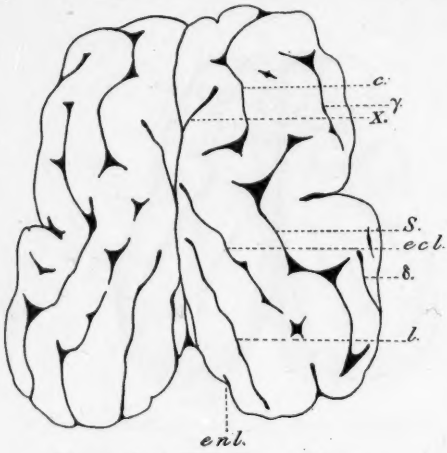


Fig. 23. Stade VIII. Face supérieure.

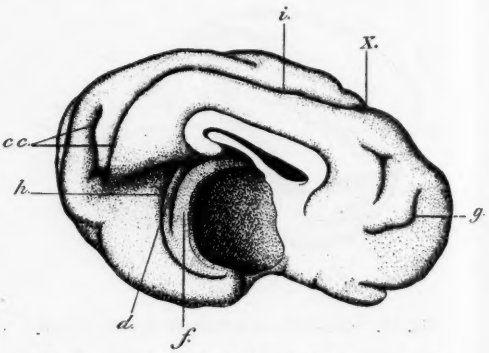


Fig. 24. Stade VIII. Face latérale interne gauche.

s'arrête, comme chez le Bœuf, avant d'atteindre la rhinale antérieure. Le sillon γ part de l'*ectosylvia*, antérieure, disposition inconstante, comme nous l'avons déjà noté. L'ectolatéral, à l'apparition duquel nous n'avons point assisté par manque du stade précis caractéristique, est extrêmement développé aussi développé que le latéral; l'entolatéral reste au contraire très petit et n'existe encore qu'à droite. Le vertical semble absent, et, en raison d'une particularité qui doit être assez rare, les deux cruciaux sont décalés l'un par rapport à l'autre, le droit étant beaucoup plus antérieur que le gauche.

Face interne (Fig. 24): La principale particularité à signaler est le développement et la complication de la partie postérieure de l'intercalaire c'est à dire de la calcarine.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 67{\cdot}7.$$

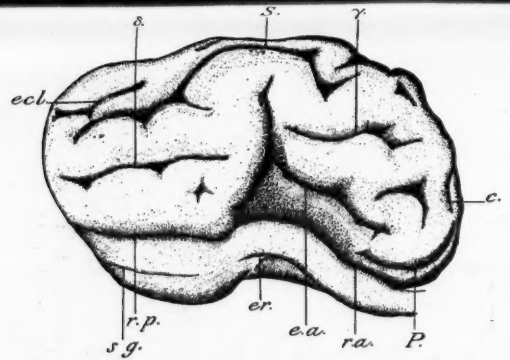


Fig. 25. Stade VIII bis. Face latérale externe droite.

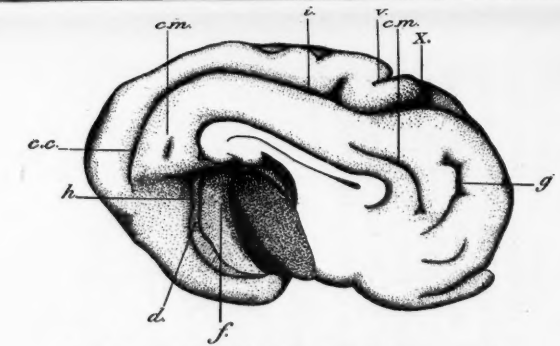


Fig. 27 Stade VIII bis. Face latérale interne gauche.

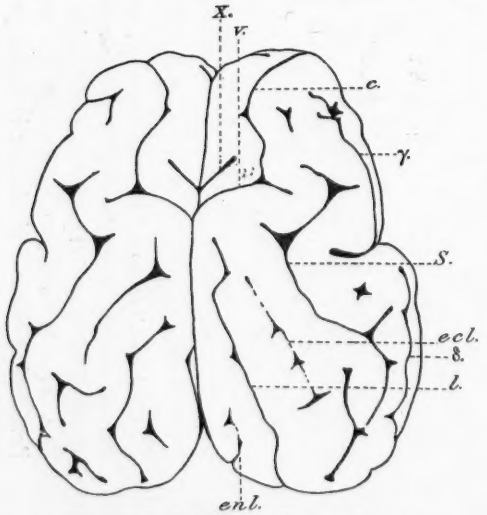


Fig. 26. Stade VIII bis. Face supérieure.

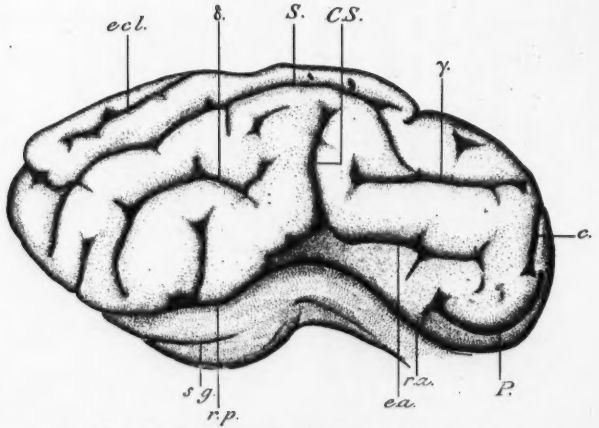


Fig. 28. Stade IX. Face latérale externe droite.

Stade VIII bis

Face externe (Fig. 25 et 26): A peu près rien à signaler, si ce n'est que l'ectolatéral ne présente pas le développement exagéré constaté sur le cerveau précédent. De plus, le vertical et le crucial ont leur aspect normal.

Face interne (Fig. 27): La partie postérieure de l'intercalaire n'est pas compliquée, comme dans le cas du cerveau précédent. Par contre, il existe une ébauche de calloso-marginal, non seulement en arrière, mais en avant; nous avons constaté l'absence de ce sillon dans la plupart des cerveaux précédents.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 63{\cdot}6.$$

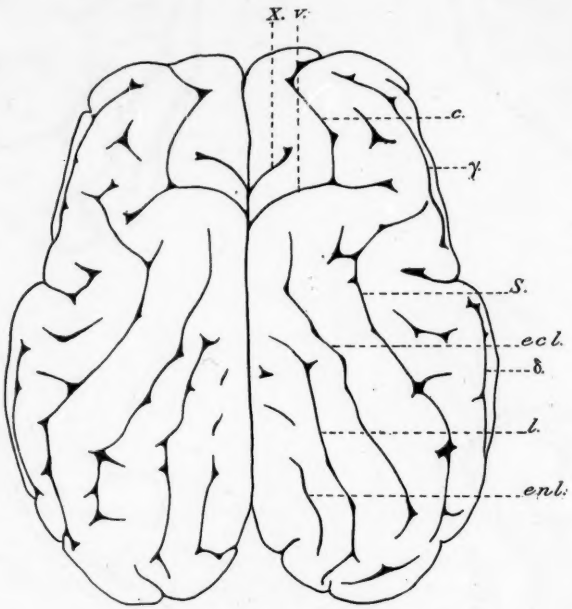


Fig. 29. Stade IX. Face supérieure.

Stade IX

C'est sensiblement l'état adulte (Figs. 28, 29, 30). Les seules différences que ce cerveau présente avec le précédent consistent en des complications secondaires. Le sillon γ n'est pas en relation avec l'*ectosylvia*, où, pour mieux dire, avec le complexe sylvien qui est maintenant complètement formé; l'ectolatéral est très développé; le calloso-marginal est bien développé, mais fragmentaire.

$$\text{Indice } \frac{\text{Haut. tél.} \times 100}{\text{Long.}} = 57{\cdot}1.$$

RÉSUMÉ ET CONCLUSIONS

En résumé, le cerveau du Mouton est du même type que celui du Bœuf, s'en distinguant pourtant, tant au point de vue de sa morphologie chez l'adulte que de la marche de son développement par un certain nombre de caractères qui ne sont point sans importance.

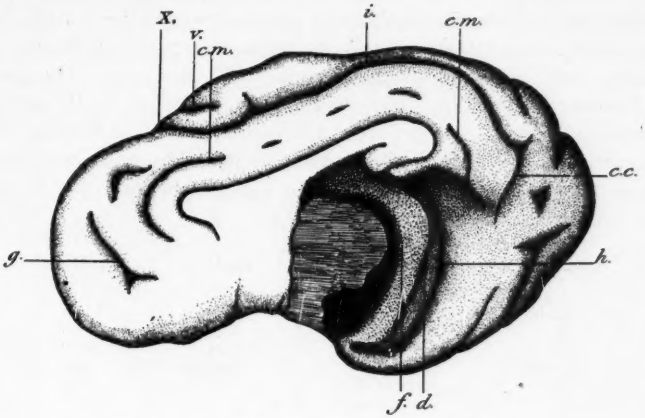


Fig. 30. Stade IX. Face latérale interne droite.

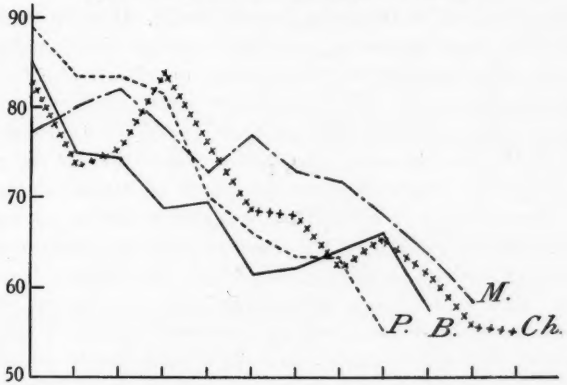


Fig. 31. Graphique destiné à montrer le développement de la forme allongée du télencéphale chez le Porc (*P.*), le Cheval (*Ch.*), le Bœuf (*B.*) et le Mouton (*M.*).

(1) Comme le cerveau du Bœuf, il est très allongé par rapport à sa hauteur. C'est une forme commune à tous les cerveaux d'Ongulés et qui s'accentue au cours de l'évolution ontogénique. Cependant, la comparaison à cet égard du cerveau du Mouton avec celui du Porc, du Cheval et du Bœuf permet de mettre en lumière un certain nombre de conclusions qu'exprime le graphique de la Fig. 31, d'une manière assez inexacte d'ailleurs, puisque les stades ne se

correspondent pas exactement d'une espèce à l'autre, en d'autres termes que les intervalles de temps ne peuvent être considérés comme étant rigoureusement égaux: Au début, le cerveau du Mouton est le plus allongé des quatre, celui du Porc étant au contraire le plus près de la forme sphèrique, ce qui doit sembler naturel, étant donné que le Porc est en quelque sorte le moins Ongulé des Ongulés actuels, ayant, à divers égards, notamment à celui de la morphologie néopalléale, des caractères le rapprochant, en une certaine mesure, des Carnassiers. A partir de ce stade de début, le cerveau du Mouton prend, de plus en plus, la forme allongée comme celui des autres Ongulés, mais l'étant finalement moins que celui du Porc, du Cheval et du Bœuf. Ceci est probablement dû, au moins en partie, à la moindre taille du Mouton. On sait en effet que, d'une façon générale, dans un groupe d'animaux comparables, le cerveau se rapproche d'autant plus de la forme sphérique que la taille somatique est plus réduite.

Stades	Indices		Stades	Indices
I	77·7		V	77·7
I bis	80·0	80·0	VI	73·0
II	80·0		VII	72·0
III	82·3	78·6	VIII	67·7
III bis	75·0		VIII *bis*	63·6
IV	72·7		IX	57·1

(2) De même que celui du Bœuf, le cerveau du Mouton est caractérisé par l'operculisation progressive du *gyrus arcuatus* No. 1. Il en est de même aussi chez le Porc; c'est donc, semble-t-il, une caractéristique fondamentale du télencéphale des Ongulés artiodactyles. Mais, alors que chez le Bœuf l'operculisation ne s'accomplit pas en fait, la première circonvolution arquée restant superficielle, et même se subdivisant en deux étages, elle s'accomplit, au contraire, chez le Mouton, de même que chez le Porc. Notons par parenthèses que, chez le Cheval, l'operculisation qui porte en avant, comme chez les Artiodactyles sur le *gyrus arcuatus* No. 1 ne porte, en arrière, que sur le rhinencéphale (lobe piriforme), d'où il s'ensuit que le sillon d'operculisation est en avant l'*ectosylvia* et, en arrière, la rhinale elle-même. Au surplus, l'operculisation n'atteint pas, chez le Mouton, le même degré de perfection que chez le Porc, le *gyrus arcuatus* No. 1 restant toujours largement visible. Il convient aussi de noter que si, chez le Porc, plus voisin des Carnassiers, le complexe sylvien est, comme chez eux, oblique de bas en haut et d'avant en arrière, il est nettement vertical chez le Mouton et, il est facile de se rendre compte de ce que, s'il existait chez le Cheval et le Bœuf, il aurait aussi cette direction verticale. Enfin, insistons sur ce fait que, si chez le Porc et le Bœuf, le creusement de l'*ectosylvia* commence par sa branche antérieure, il commence par sa branche postérieure chez le Cheval et le Mouton.

(3) L'apparition de la calcarine est chez le Mouton très tardive; c'est un fait commun, non seulement aux autres Ongulés déjà étudiés, mais aux Carnassiers, l'ensemble de ces animaux se différencient à cet égard des Pri-

mates où le creusement, sinon de la calcarine, mais de la retrocalcarine (fosse striée) est, au contraire, extrêmement précoce.

(4) Comme chez le Bœuf, le crucial apparaît, chez le Mouton, à une époque très tardive; mais il est à remarquer que ce sillon est beaucoup plus développé et plus typique chez le Mouton que chez le Bœuf.

(5) La *presylvia* est courte chez le Mouton, comme chez le Bœuf.

(6) L'ectolatéral a une beaucoup plus grande importance chez le Mouton que chez le Bœuf, arrivant même à prendre les dimensions et l'aspect du latéral. Nous n'insisterons pas sur les différences dans l'ordre de succession des sillons que présente le Mouton par rapport au Bœuf.

Indications relatives aux figures.

Néopallium: *S.* Suprasylvia.
e.a. ectosylvia antérieure.
e.p. ectosylvia postérieure.
P. Presylvia.
l. latéral.
ecl. ectolatéral.
enl. entolatéral.
c. coronal.
V. Vertical.
Cc. Calcarine.
i. intercalaire.
g. genualis.
γ. sillon γ.
δ. oblique de G. Elliot-Smith.
cm. calloso marginal.
X. crucial.
Rhinencéphale: *r.a.* rhinale antérieure.
r.p. rhinale postérieure.
er. endorhinale.
h. fissura hippocampi.
d. gyrus dentatus.
f. fimbria (fornix).
sg. sulcus sagittalis.
t.o. tubercule olfactif.

Toutes les figures sont au double de la grandeur naturelle.

INTRA-EPIDERMAL NERVE ENDINGS

By H. H. WOOLLARD
St Bartholomew's Medical College

It has been generally accepted that the epidermis is the seat of the sensation of pain and the dermis the seat of the sensation of touch.

This belief, of some duration, was made stronger when v. Frey (3) placed the notion of the punctate distribution of the elementary cutaneous sensations on a firm basis. The localization of pain depended much on the statement that the cornea in its central part experiences pain only, and that it is here that naked nerve terminals of the corneal nerve plexus, having become first hypo-epithelial, continue on amongst the epithelial cells of the conjunctiva. The two conclusions—that pain depends on the fine naked nerve terminals and that its seat is in the epidermis, continued henceforth to be acceptable.

Quite recently they have been challenged by Waterston (9), and he has emphasized two observations in particular as supporting the contrary opinion that the epidermis is not the seat of pain, but is really the seat of touch. He has stressed the fact that the threshold value for touch is so small that it is not conceivable that the sensory apparatus for touch can lie buried below the many layers of the epidermis. In fact he asserts that organs like Meissner's corpuscles are not organs of touch but really organs of pain. It is obviously a matter for investigation what the threshold for touch is and whether the stimulus is too small to reach the dermis. Since the evidence is good that touch is only aroused by a deformation of the skin, the argument derived from the threshold value of touch as to its anatomical place in the skin does not seem a very strong one.

The second observation of Waterston depends on the fact that it is possible to shave off at least the greater part of the stratum mucosum of the epidermis without causing any pain at all, but only the sensation of touch. This second argument seems to us a much more important one.

It is to be remarked that no matter whether one accepts the epidermis as the seat of pain or as the seat of touch, in either case one would expect an overwhelming abundance of nerve fibres in the epidermis. For if one marks out on any part of the surface of the body the points sensitive to touch by means of v. Frey hairs and of pain by means of the prick of a pin, one is overwhelmed by the multitude of responding points. Indeed if the theory of the punctate distribution of the cutaneous sensations had to depend only on such observations as these, its hold upon us would be much less firm. It is therefore most pertinent to enquire if such rich epidermal innervation exists.

Before turning to our own observations a brief survey of the findings of others is of importance, since many investigations have been made on the intra-epidermal nerve endings.

The distinction of Retzius as an investigator and the wide extent of his observations seem to be the reasons why it is generally assumed that the epidermis is beset with an abundance of naked nerve terminals. In the skin of the cyclostomes, salamander and other non-mammalian forms, he has published figures of a rich plexus of naked terminal in the epidermis. In mammals, though a similar state has been assumed, nothing of the sort has ever been found. The cornea and mucous surfaces we may leave on one side for the moment, as being not comparable with ordinary epidermis, since their surfaces are always moist. In lower mammals such as the rabbit, it is possible to find more easily than in higher forms a number of epidermal nerves, but in general it can be asserted that in mammals and especially in man in the ordinary epidermis it is very difficult to find intra-epidermal nerves, and no one has figured any extensive and abundant epidermal plexuses. The Spanish school (Tello) have remarked that in man they are more common in the epidermis of the foetus and that they disappear later. Agabow (2) has even denied their presence. Others comment on the difficulty of finding them.

ENDINGS FOUND IN EPIDERMIS

The form and situation of those epidermal nerves which have been found by many investigators have been described in a remarkably uniform manner. They are found in the snout and muzzle of animals like the pig; in Eimer's organ—a relatively huge and specially designed epicritic organ in the deer; in the hand and soles of the feet in man; in the outer root sheath coverings of the hair follicle. It is to these regions most descriptions have applied. It is from the observations in these regions that by inference and assumption the same is regarded as applying to all epidermis. This restriction, not of course absolute, is, as a critical survey of the literature discloses, a most prominent one.

It is customary for most authors to allude to naked terminals in the epidermis. These we have seen but they are uncommon. Very few descriptions of them have been made from human skin. Most observations have been made on facial and snout skin in the ungulates. Kadanoff (4, 5, 6), who has given the best description of them in recent times, based his observations on the snout of the deer.

The other commoner forms upon which all can agree are at least two. One is the general occurrence of Merkel's discs. These have been found in the deeper layers of the stratum mucosum generally in all parts of the body, but most abundantly in parts like the hand, lips, etc., which are already distinguished for their high degree of tactile acuity. These endings are the offspring of well-medullated fibres, but the best reason for accepting their tactile office is the fact that they are frequently borne on the continuation of the neurofibrillae of Meissner's corpuscles.

These continuations pass on into the epidermis, and there form these Merkel's discs. It is still at any rate a credible idea that a nerve fibre subserves

one kind of sensation and one only, and if Meissner's corpuscles are for touch then these discs are of necessity also for touch. The abundance of Meissner's corpuscles in the hands and feet in man and the anthropoids make it difficult to accept any other functional allocation for them; to say nothing of all our notions about the primitive simplicity of pain suggesting a similar unpretentiousness in its anatomy.

Medullated fibres form some sort of spiral ending in many of the papillae of the dermis. These are thought to be a very simple form of a Meissner's corpuscle. It is a common observation that from such fibres terminals are continued to the stratum Malpighii. They do not pass much beyond this in the epidermis. Usually they end about the epidermal cells in some sort of an expansion resembling a Merkel's disc. These again suggest a tactile function. No one has ever suggested for hairs any other function in cutaneous sensation than that of increasing tactile acuity. It is an observation that helps our suggestion that the intra-epidermal endings are associated with touch for Merkel's discs, and even more elaborate endings are found in the outer root sheath of hairs.

Thus we want to stress the fact that no one has claimed in man to have found abundant intra-epidermal innervation either of the naked terminal kind which would suggest pain or of a more organized kind that would suggest touch. The naked terminals of pain we would not exclude absolutely, but we believe it to be uncommon. In those parts of the body especially where tactile acuity is high, and in other parts, much less abundantly, epidermal endings are to be found often in themselves well organized, often traceable to medullated nerves, and finally perhaps the continuations of especially intricate structures like Meissner's corpuscles.

We thus come to the conclusions that the epidermis is not in any way the special site of pain. We agree with Waterston that it is an organ of touch. Waterston, however, goes too far in emphasizing it as the exclusive organ of touch. We see it rather as an accessory organ of touch.

Obviously such an opinion would be more secure if we could find a sufficiently abundant terminal nervous apparatus conforming to our ideas of what ought to be the anatomy of a pain plexus, and situated in a place that satisfies the requirements of experimental observations.

EXPERIMENTAL OBSERVATIONS

It is a fact that much of the epidermis can be shaved away without exciting at any rate a severe sensation of pain. Mr McIndoe with a razor used for cutting grafts made three slices along the outer side of the thigh in a particular subject before it was necessary to resort to local anaesthesia. Before the cuts were made a map had been constructed of the points from which touch, cold and pain could be elicited with the least stimulus. This map could be superimposed on the skin after each cut.

When the knife was traversing the epidermis an attempt was made to correlate the situation of these spots, where a light prick elicited the most severe pain with the exclamations made by the subject on his sensations of pain. Though such an experiment is fraught with many difficulties it was claimed that this was done with considerable success, and it was agreed that the exclamations coincided with the cutting through of the marked pain spots. These points of severe pain were found further to coincide with the cutting through of the papillae of the dermis. The oozing from the capillary loop in the dermis indicated that this was what had happened. The later cuts which severed many capillary loops, and this was passing through more and more of the subepidermal tissues, were so violently painful that cutting without an anaesthetic was out of the question.

These experiments which agree with the observations of Waterston (9) suggest that an abundant pain plexus should be found above all in the subepidermal region.

Pain is a sensation that relatively is poorly localized, that irradiates widely and lacks discriminating value. In those situations where it is the only elicitable sensation, it has the form of fine varicose fibres without ensheathment and forming no complex kind of ending. The results of experiments such as those of Ranson (7) that pain is conveyed by non-medullated or finely medullated fibres have on the whole been accepted. The study of the action potentials of single nerve fibres, thresholds, rates of conduction, etc., all point in the same way to the pain nerves being subserved by a much finer and simpler anatomical structure than that of the other sensations. It is only fair to point out that the physiological and anatomical results are not altogether in harmony on this matter, nor can the restriction of pain conduction to the finest nerve fibres be regarded as proven.

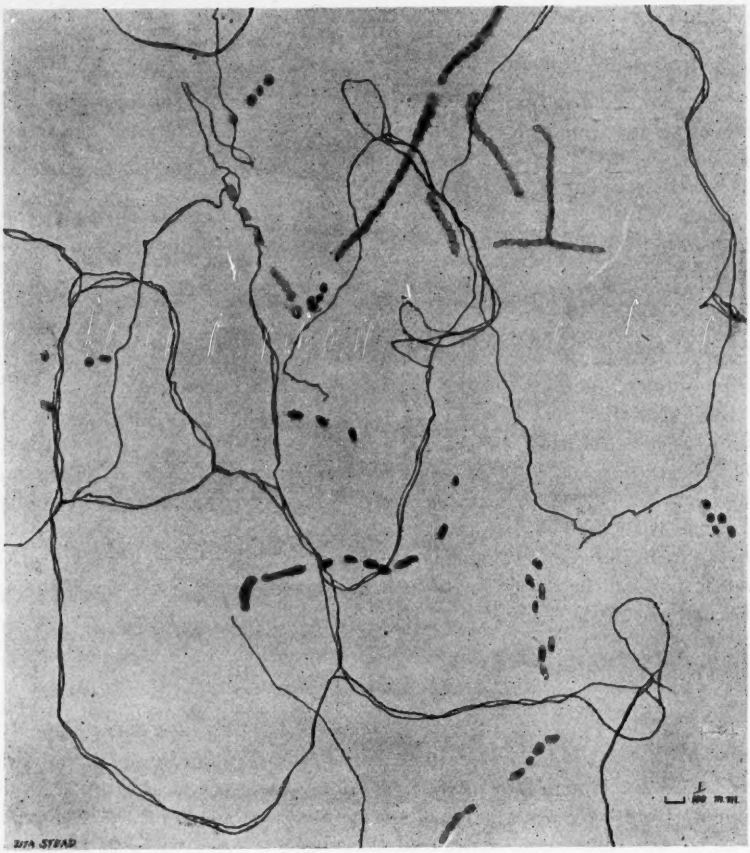
ANATOMICAL OBSERVATIONS

Pl. III, fig. 1, which is an actual photomicrograph of a nerve plexus discovered in a subepidermal position, is regarded as affording the anatomical basis for pain. This nerve apparatus is composed of the finest fibres. As they come up from the deeper layers of the dermis they are about 3 μ in diameter. Soon on becoming more superficial they become finer still and assume the dotted irregular varicose form. The filaments so formed have a marked tendency to run in the form of a closed loop. These loops have been most carefully examined, and at times actual fusion of neurofibrillae occurs and so a closed loop is formed. Frequently, however, single fibres come to an end. This mode of termination is regarded as the actual ending of the nerve fibril. The endings achieve no complexity and for a considerable distance they are naked neurofibrillae without ensheathment of any kind.

This plexus occupies a subepidermal position immediately below the stratum Malpighii, and can be found presumably all over the body in this position. Our

own observations have found it in many places in the upper and lower extremities.

Occasionally some fibrils can be traced into the epidermis but this is rare. One drawing (Text-fig. 1) is included to exhibit this uncommon impingement



Text-fig. 1. A drawing of the plexus of fine beaded fibres ramifying at the subepidermal level. There are points at which the plexus appears to be reinforced from below. Discs indicate capillaries and red blood corpuscles. Methylene blue. Human skin from amputated leg. × 284.

on the epidermis. Similar terminal fibres to these are found throughout the dermis, and they are also present as an additional or accessory fibre to more highly organized endings. Many have described these, and we have observed them in relation to Meissner's corpuscles, in relation to hairs, and Pacinian corpuscles, Krause end bulbs and the like. Some have jumped to the con-

clusion that these fine accessory fibres belong to the sympathetic nervous system. It is more probable that they belong to the pain system and act as protective nerves to these more complex endings.

Experimentally we have felt that the evidence suggested that the anatomical situation of pain begins at the subepidermal level. The discovery in that situation of a plexus and endings in sufficient abundance and of the appropriate character reinforces the experimental conclusion.

Thus we come to regard the epidermis as being accessory to touch, this being more especially the case in regions where tactile acuity is high. Intra-epithelial neurofibrils and endings are figured as occurring abundantly in such places as the conjunctiva and the mucous membranes of the mouth, pharynx and larynx. Even if this be so we regard the innervation of these surfaces as distinct from that of the epidermis and offering no grounds for the belief that this also would enjoy a similar richness of nerves.

SUMMARY

1. Experimental and anatomical evidence suggesting that the epidermis in man is only occasionally accessory to pain is discussed.

2. Evidence for the appearance of touch endings, especially in places of high tactile acuity, is mentioned.

3. The discovery of a terminal nerve apparatus in which both free ends and continuity of neurofibrils occur agrees with the anatomical and experimental evidence that pain is immediately subepidermal.

I am indebted to Miss Z. Stead for the drawings, the photographs and the skilled assistance that make such an investigation as this possible.

REFERENCES

(1) Adrian, E. D. (1932). *The Mechanism of Nervous Action.* Oxford University Press.

(2) Agabow, A. (1912). "Über die Nerven in den Augenhauten." *v. Graefes Arch. Ophthal.* vol. LXXXIII, p. 317.

(3) Frey, M. v. (1926). "Die Tangoreceptoren des Menschen." *Handb. normalen path. Physiol.* Bd. XI, pp. 94–130.

(4) Kadanoff, D. (1924). "Beiträge zur Kenntnis der Nervendigungen im Epithel der Säugetiere." *Z. anat. Entw.-gesch.* Bd. LXXIII, pp. 431–52.

(5) —— *Über die Innervation des Mesenterium,* p. 453.

(6) —— (1928). "Über die intraepithelialen Nerven und ihre Endigungen beim Menschen und bei den Säugetieren." *Z. Zellforsch.* Bd. VII, pp. 553–76.

(7) Ranson, S. W. (1931). "Cutaneous sensory fibres and sensory conduction." *Arch. Neurol. Psychiat.*, Chicago, vol. XXVI, pp. 1122–44.

(8) Tello, J. F. (1932). "Contribution à la connaissance des terminaisons sensitives dans les organes génitaux externes et de leur développement." *Trab. Lab. Invest. biol. Univ. Madrid,* T. XXVIII, pp. 1–59.

(9) Waterston, D. (1933). "Observations on sensation." *J. Physiol.* vol. LXXVII, pp. 251–57.

(10) Woollard, H. H. (1935). "Observations on the terminations of cutaneous nerves." *Brain,* vol. LVIII, pp. 352–67.

EXPLANATION OF PLATES I–III

Plate I

Fig. 1. Fine varicose naked terminals in the epidermis. Methylene blue. Counter-stained carmine. Human thigh. 10 μ section. ×2000.

Fig. 2. Merkel's discs formed from medullated fibres in the dermal papillae. Cajal's silver method. Human thigh. 10 μ section. ×1200.

Fig. 3. Intra-epidermal nerve fibre extending to the stratum granulosum of the epidermis. Note immediately below the stratum Malpighii the thick transversely running nerve fibre from which the intra-epidermal fibre starts. Cajal's silver method. Human skin. 10 μ section. ×212.

Fig. 4. Intra-epidermal nerve fibre extending to the stratum granulosum of the epidermis. Cajal's silver method. Human thumb. 10 μ section. ×212.

Plate II

Fig. 1. A photomicrograph of heavily medullated thick fibre. Its termination and the dense flocculated and spiral endings are seen. From the termination of ordinary Meissner's corpuscles further extensions into the epidermis occur where they end as Merkel's discs. Methylene blue. Human skin. Amputated leg. ×300.

Plate III

Fig. 1. A photomicrograph of the subepidermal plexus. The tendency to form a neurofibrillar net and occasional free endings is seen. It is composed of the finest beaded fibres. The cells seen between the fibres are red blood corpuscles. Methylene blue. Human skin. ×315.

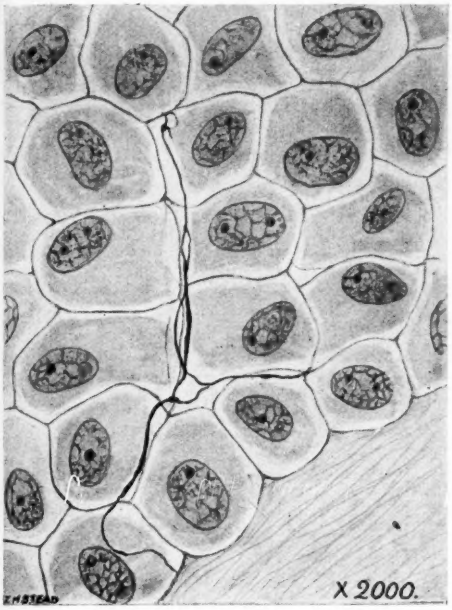


Fig. 1.

Fig. 2. ×1200.

Fig. 3. ×212.

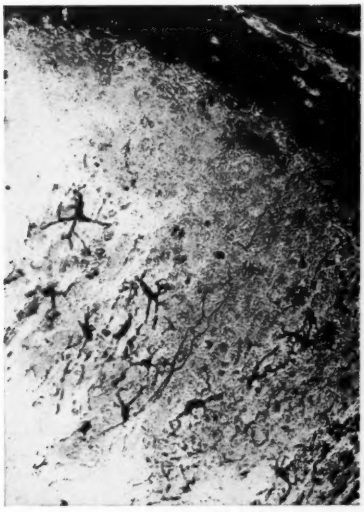
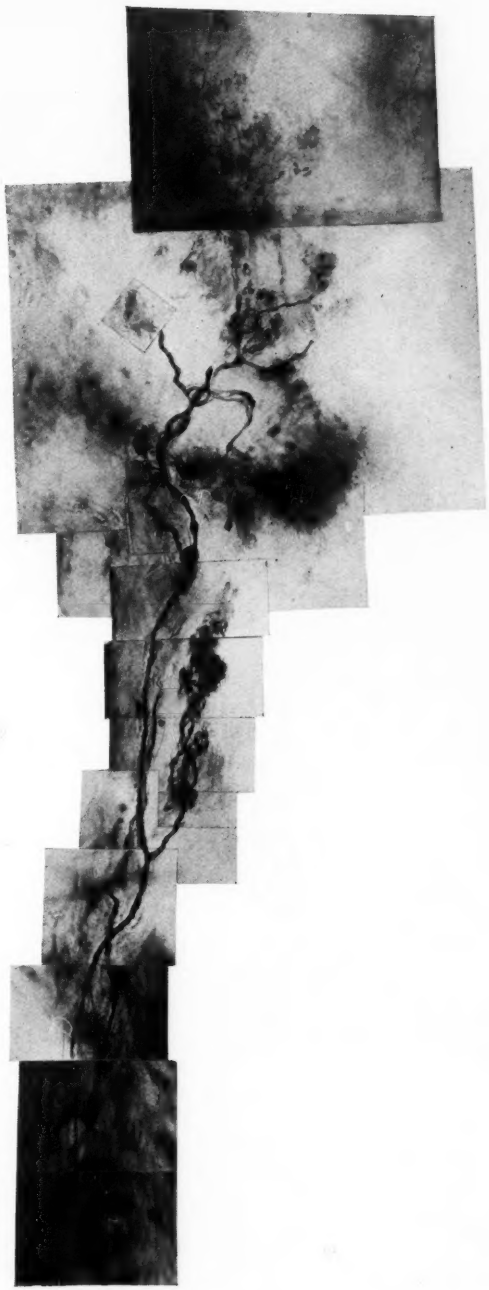


Fig. 4. ×212.

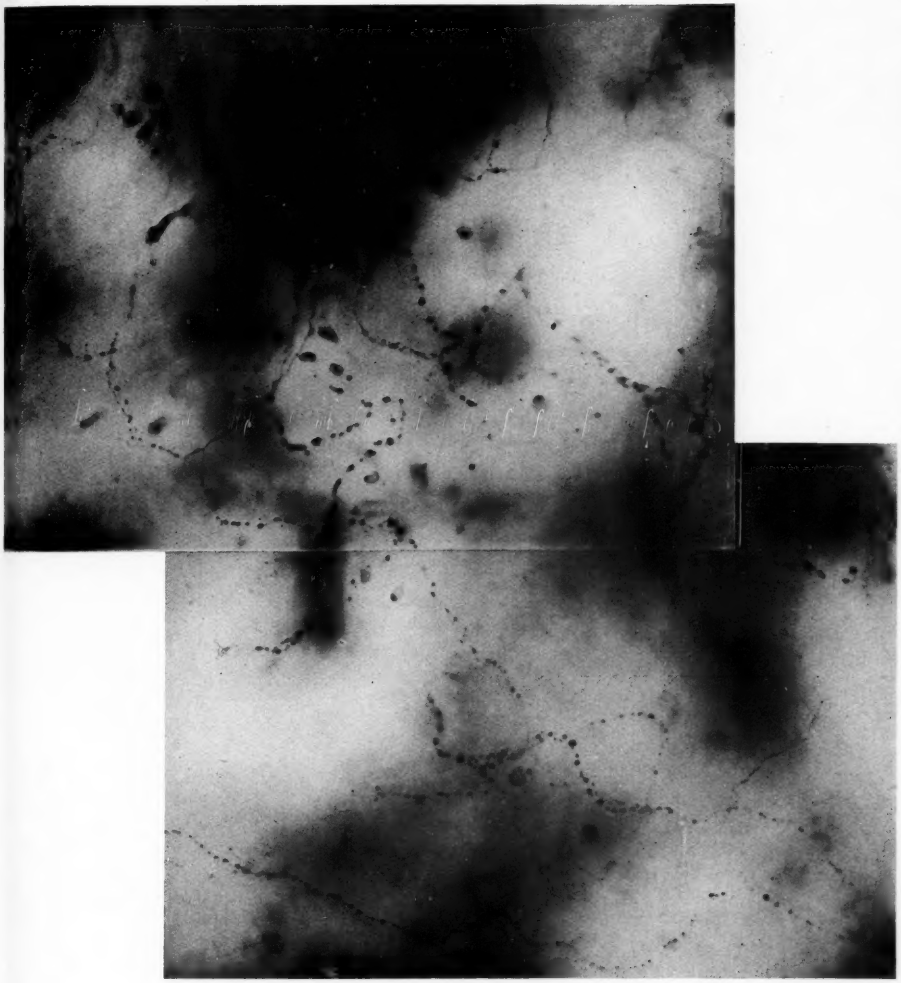
UNIV. OF MICH.



×300.

WOOLLARD—Intra-epidermal Nerve Endings

UNIV. OF MICH.



×315.

UNIV. OF MICH.

THE ENDOCRANIAL CASTS OF THE EHRINGSDORF AND *HOMO SOLOENSIS* SKULLS

By C. U. ARIËNS KAPPERS

It is a great honour to me to contribute a paper to this issue of the *Journal of Anatomy*, dedicated to Prof. Sir Grafton Elliot Smith, whose lines of work and interesting results so strongly influenced the direction of my own work, which in later years frequently took paths marked out before by him.

When—thirty years ago—I entered Edinger's laboratory, my new chief told me that I was entirely free to work on any subject I liked in comparative neurology, provided I did not deal with gross anatomy and fissuration of the brain. This remark was not so strange as it may look, since this was in 1906, when better staining methods for the first time enabled us to take up the study of the lower vertebrate brain, a field opened up by Edinger.

When I returned to Amsterdam, and came into close contact with the English leader of neuro-anatomy I was, because of this earlier experience, impressed by his all-round knowledge and broad view of neurological problems, problems of comparative morphology and fissuration of the brain rather neglected since Campbell's, Brodmann's, Mott's and Vogt's valuable work on cyto- and myelotectonics.

Prof. Elliot Smith's work, e.g. his descriptive catalogue of the collection of the Royal College of Surgeons, his contributions on the cerebellum, on the occipital lobe in the Egyptian and other brains, his macroscopic tracings of cortical fields, the correlation between tectonic regions and fissuration, his studies on simian and human cerebral features, his work on the lunate sulcus, and his microscopical studies, could not fail to impress all those interested in more general aspects of brain anatomy; the more so as several of his most striking results were obtained in fields of neuro-anatomy that had been open to anatomists for more than a hundred years.

Not less stimulating was his influence on those interested in ethnology and in anthropology. How many of Elliot Smith's pupils have followed their master also in this field and how much they contributed to it, is well known. Indeed, few anatomists created such a great and excellent school as he did. Pupils of his are found in all continents and everywhere belong to the best and most active workers.

Considering the main lines of Elliot Smith's own work it may not be inappropriate if in this volume I deal with a subject combining brain anatomy and anthropology. However scanty the information given in the following pages may be, it concerns a subject the importance of which has been fre-

quently emphasized by Elliot Smith himself, as in his paper "Casts obtained from the brain of fossil men" (20) and in the paper published with Shellshear on the endocranial cast of *Sinanthropus pekinensis* (19), discovered by his pupil Davidson Black.

THE ENDOCRANIAL CASTS OF THE EHRINGSDORF AND NGANDONG SKULLS

Although Weidenreich (24) already gave a very detailed description of the Ehringsdorf skull and also other authors (e.g. Hrdlicka (7)) dealt with it, hitherto no description of its endocranial cast has been given.

This skull was found in the same stone bed from which previously an adult human under-jaw and various remains of a child about 10 years old were obtained. The skull, found in 1925, was not complete. Apart from the calotte (24), p. 51) only a part of the left temporal bone was found. Besides, the skull was pressed and its bones separated along the sutures. Since such a separation is possible only if the sutures have not yet been strongly ossified, the individual was estimated to be between 20 and 30 years old. The gracility and the faint muscular insertions made Weidenreich think that it was a female skull. Like the jaw and teeth found earlier (Schwalbe (18), Virchow (22), Boule (3) and Keith (11)) this skull showed distinct Lower Palaeolithic affinities, resembling the Neanderthal, both Spy skulls, Krapina segments and the La Chapelle skull ((24), p. 71).

In some respects, especially in its frontal and medial vaulting, the calotte ((24), p. 100) surpasses the average of the Neanderthal type, having more in common with the Upper Palaeolithic Cro-Magnon type from which, however, it differs again in other respects, e.g. by its lesser parieto-occipital vaulting.

The chief measurements and indices of the Ehringsdorf skull are: greatest length 196 mm.; greatest breadth 145 mm.; cephalic index 74; inside length 171 mm.; inside breadth 134·5 mm.; L.H. index 61·7; Br.H. index 83·4; calotte height over the glabello-inion line 96 mm.; glabello-inion length 192 mm.; calvarial height index 50; positional index of the bregma 29·9; bregma angle 56°; transverse fronto-parietal index 77·9; glabella cerebral index 38·6; inter-orbital index 24·6; frontal angle 79°.

The inside length of the skull being 171 mm., its inside breadth 134·5 mm., this gives an endocranial index of 78·6. The capacity was estimated 1450 c.c., i.e. considerably more than the female La Quina (1350 c.c.) and female Gibraltar skull (±1300 c.c.).

Through the kindness of Prof. Klinghardt, Berlin, we obtained an endocranial cast of the skull (Fig. 1). The first thing to impress us is the asymmetry of the cast as seen from above the left parieto-occipital lobe bulging out far more than the right. The same is seen on the exocranium ((24), fig. 39). Weidenreich believes this to be due to influences acting on the right parietal after the skull has been imbedded in the layer in which it was found. Since

Fig. 1. Ehringsdorf cast (Weidenreich). Lower figure 0·42 of real size.

the left side of the cast is the most normal and also the most complete, I shall use this side for my description.

Calculating the encephalic index with the length and the double of the maximum breadth of the left hemisphere gives 78·3, i.e. only 0·3 point less than the inside index found by Weidenreich and 4·3 more than the exocranial index (74) as given by this author. Comparing the exocranial indices of some other Palaeolithic skulls with their endocranial index, we find also great differences:

L. Br. index	*Sinanthropus*	Düsseldorf	Spy I Spy II	La Chapelle	La Quina	Rhodesian	Gibraltar	Ehringsdorf	Ngandong V
Sex	Female	Male	Male	Female	Female	Male	Female	Female	Male
Exocranial index	73·56 Black (2)	73·8 (2)	72·1 (I) 77·4 (II)	75·0 Boule	68·2 Hrdlicka	71·8 Hrdlicka	77·0 Hrdlicka	74·0 Weidenreich	65·2* Oppenoorth
Inner cranial index (Br. 122 ?)	77·7? R. 78·2? L. Black (2)	—	77·1 (I) 82·4 (II) Hrdlicka	—	—	—	—	78·6 Weidenreich	—
Endocranial cast index†	76·92 (R.) 77·26 (L.) *77·09*	79·3 *79·7* Anthony	—	78·3 *79·0* Anthony	73·8 *74·3* Anthony	79·84 *79·13*	81·5?‡ Anthony 80·0?	78·3	77·1*

* The index 65·2 is calculated with the max. length, the index 67·09 with the length to the torus occipitalis.

Since this was written Mr Oppenoorth kindly informed me that the reconstruction of the skull, made after this endocranial cast was made, decreased the outside length of the skull by about 2 mm., due to the closing up of clefts between the sutures. This would make the exocranial index calculated with max. length 65·7, with length to the torus occipitalis 68·5. Accepting the same reduction for the length of the endocranial cast would make the endocranial index 77·2. The difference between the exo- and endocranial index, however, remains very great (about 10). The absolute height of the skull has not changed.

† The smallest figure of this series is calculated with the length of the greatest hemisphere, the italicized figure with the mean length of both hemispheres.

‡ It seems to me that Anthony's index calculated on the largest hemisphere for which he found a length of 168, with a total breadth of 137, is too large. My figure for this hemisphere is 79·7.

From this table it appears that the differences between the exocranial indices are much greater than those between the endocranial indices. The greater variations in the exocranial index are due to the differences in the glabellar protrusion which runs more or less parallel to the development of the frontal sinus and the supra-orbital ridges.

Another factor, though less important, is the different thickness of the skull in both directions. With the Rhodesian the exocranial dolichocephaly is still enhanced by a considerable torus occipitalis, and this may be more so with the *Homo Soloensis* (Ngandong) V (Oppenoorth (14)). On the other hand, it is interesting to note that—apart from the La Quina cast—the endocranial indices in our table only vary between 77 and 80.

The difference between the exo- and endocranial index has a much wider range in Palaeolithic than in modern man. While this difference in the Düsseldorf skull is 5·9, in both Spy skulls 4·7 and 5·4, in the La Chapelle skull 4·0, in the adult female La Quina skull 4·3, in the Rhodesian 7·33, in the female Gibraltar skull 3, in the Ehringsdorf skull 4·3, in fifty-three Irish Keenan (10) found a difference of 2·4 taking the length of the shortest hemisphere and 1·3 with the length of the longest. From Wagner's ((23), p. 102) data it appears

that the difference between the outer and inner L.Br. index (in favour of the inner index) for Norwegian skulls is 1·60 (♂ and ♀); for Lapps 1·56 (♂) and 0·60 (♀); for Maori 3·25 (♂) and 1·29 (♀); and for Australian skulls 3·97 (♂) and 32·5 (♀).

The average difference in these Lower Palaeolithic skulls is 4·85. That in *Sinanthropus* this difference according to Black's measurements is 4·39 (according to my endocranial cast even less: 3·53) may be due to its young age and female sex.

Considering the fact that the greater difference and also the greater variability in Neanderthal man is due to the external excrescences of the cranium, it is not strange that in anthropoids they are still greater and also more variable, especially in the males where these excrescences are largest. Besides, whereas in man the exocranial index is always the smaller one, Harris (6) found it larger in eleven out of thirty-nine male gorilla skulls. In the other twenty-eight male skulls the variation in favour of the endocranial index was very great.

Even among his twelve female gorilla skulls Harris had two cases in which the exocranial index was somewhat though little larger. In the remaining ten skulls the exocranial index varied from 75·1 to 79·4, the endocranial from 79·1 to 85·2, the average difference in favour of the endocranial index being 6·02.

The Ehringsdorf endo-exocranial difference being 4·6, or—according to my cast—4·3, remains below the average of Neanderthal men.

The difference between the exo- and endocranial index runs parallel with what Weinert (25) calls the cranio-cerebral index, i.e. the relation between the outside and inside length, the latter being measured not in the mid-sagittal plane but on both sides next to it where it is greater. The adjoining figures for this index are given as calculated after the data of the submentioned authors.

Gorilla	Chimpanzee	*Pithecanthropus*	*Sinanthropus*	Ngandong* V	Spy I	Spy II	Average 14 Neanderth. skulls	Ehringsdorf	Australian	European
75	81	83·7	83·6	83·97	84·9	85·5	86·0	87·2	88·5	90·5
Weinert	Weinert	Dubois	Black	Oppenoorth	Hrdlicka	Hrdlicka	Weinert	Weinert	Weinert	Weinert

* This figure is obtained by using the maximum length to the torus occipitalis (21·2) before the reconstruction, mentioned in note *, p. 4. After the reconstruction this figure, assuming that the inner length also diminished 2 mm., should be 83·8. For Ngandong I this figure would be about 84·4, taking the length of the endocranial cast as inner length.

Austr. ♂	Austr. ♀	Maori ♂	Maori ♀	Norw. ♂	Norw. ♀	Lapp ♂	Lapp ♀
89·24	90·19	91·64	93·35	91·78	92·61	93·79	94·50
Wagner	Wagner	Wagner	Wagner	Wagner	Wagner	Wagner	Wagner

As was to be expected also in this respect, the Ehringsdorf skull stands higher than the average Neanderthal skulls.

The general height index of the Ehringsdorf cast is 0·508. Comparing it with the height indices of *Pithecanthropus*, *Sinanthropus*, Neanderthal and Predmost casts examined before (*loc. cit. infra*) this figure is rather high,

approaching the general height index of the Upper Palaeolithic Predmost casts.

Pithecanthropus	*Sinanthropus*	Ngandong V*	La Chapelle	Ehringsdorf	Rhodesia	Average	Predmost
0·400	0·453	0·456	0·477	0·478	0·508	0·516	3·4·10

* Since the absolute height of the endocranial cast has remained the same after the reconstruction, its reduced corrected length gives an increase in the general height index which by Oppenoorth was calculated to be 0·464.

This index is measured by dividing the greatest perpendicular height by the length of the cast, projected on the lateral horizontal. This is the line passing underneath the orbital protrusion (the latero-ventral border of the operculum orbitale) and the occipital pole (cf. Figs.). On this line the perpendiculars along the frontal and occipital pole are drawn and the greatest (centro-parietal) height. In my photos I also drew the temporal depth perpendicular and a perpendicular along the deepest point behind the orbital protrusion, corresponding more or less with the post-orbital narrowing of the skull.

Since in the equally female La Quina cast the orbital protrusion is not complete, I could not exactly calculate the height index for this specimen, but Fig. 2, in which the circumference of the left La Quina hemisphere after H. Martin (13) and Anthony (1) is superimposed with equal length upon the

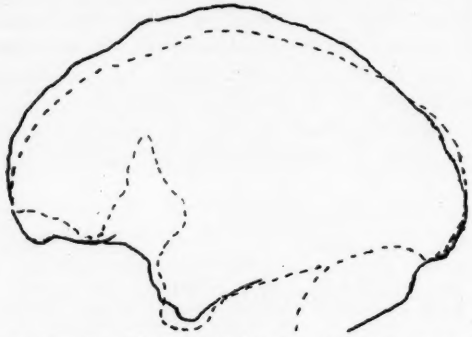


Fig. 2. Continuous line Ehringsdorf, dotted line La Quina endocranial cast.

circumference of the left Ehringsdorf hemisphere, shows that the Ehringsdorf cast is considerably higher than the La Quina cast, and that this difference in favour of the Ehringsdorf brain is especially marked in its frontal and centro-parietal parts as agrees with the external skull contours drawn by Weidenreich ((24), Fig. 40).

The lateral horizontal gives us also means of estimating the development of the rostrum orbitale (*bec encéphalique* of French authors).

It is well known that a very pronounced rostrum orbitale, due to the relative large size of the eyes (orbits) compared to the brain (case), is an anthropoid feature. In recent human brains, where it may attain a somewhat greater extension in the Eskimo and Australian, the rostrum is smaller than the

Neanderthal casts, as already stated by Boule & Anthony (4) for the La Chapelle cast. In the Rhodesian and *Sinanthropus* cast it is still more developed and also extends over the lateral horizontal, as it constantly does in anthropoids.

If we remove the fairly great amount of additional plaster (see front photo, Fig. 1) from the left rostrum of the Ehringsdorf cast, it appears that it is not nearly as pronounced as it is in the La Chapelle, Rhodesian and Ngandong V cast.

Another more advanced feature of the Ehringsdorf cast is the rather steep rise of the frontal lobe and its relative bluntness seen from the dorsal side (Fig. 1).

Besides, the postorbital narrowing in the Ehringsdorf cast is not very pronounced. Similarly the relatively small temporal depth (compared with this depth in *Sinanthropus* and the La Chapelle cast) is not primitive, nor the rather horizontal direction (less rising course) of the lower border of the temporal lobe correlated with it. As far as may be seen in this incomplete region, there is no pronounced turning in of the temporal lobe. All these facts confirm Weidenreich's opinion that this is not a very primitive representative of the Lower Palaeolithic type.

Its shape certainly is less primitive than that of the La Chapelle, Rhodesia and Ngandong V cast, whose endocranial cast contours are drawn in Fig. 6.

Unfortunately the impressions visible on the cast are too doubtful and too incomplete to allow any conclusion concerning its fissuration.

In front only the perpendicular branch of Wernicke fronto-marginal sulcus (our No. 9) may be indicated on both sides (especially on the right) and on the left a groove underneath and in front of the protrusio orbitalis may indicate a subfrontal sulcus (No. 1 of our enumeration).

For the endocranial cast of the Ngandong V skull I am indebted to the Mining Department, Bandoeng, Java, to which I express my thanks.

A preliminary description of the series of Neanderthaloid skulls found in the Solo Valley, Java, was given by Oppenoorth (14) who calls the Ngandong V skull a compressed calvarium,[1] somewhat larger than the Ngandong I skull but less complete. The basis from the nasion to the planum nuchale is wanting. The greatest length is about 221 mm. (the reduced length with correction of the torus occipitalis 212), the greatest breadth 144 mm., outside index with greatest length 65·2, with corrected length 67·9; inside length 178; glabello-inion length 216 (?), height of the calotte 87, calvarial height index 40·27; glabello-bregma angle 43°. The capacity of the skull—which is considered a male one—is about 1300 c.c.

The skull shows a considerable postorbital narrowing with a postorbital

[1] The compression of the calvaria chiefly affected the right temporal region, as is also visible on the endocranial cast. For the slight correction of the figures necessary after reconstruction I refer to pp. 64 and 66.

index of 18·1 and a strong torus occipitalis, both primitive features. It is evidently Neanderthaloid.

Since hitherto only some preliminary descriptions together with some excellent photographs of the *Javanthropus* skulls have been published, more details concerning the Ngandong V skull cannot be given here. Oppenoorth states that the parts of this skull broken by the compression fitted very well, so that we may accept that the side view he gives of this skull represents the natural condition. On this side view the large supra-orbital ridges, the flattening of the frontal part of the skull and the torus occipitalis are very striking. The calvarial height index (40·27) is lower than in Ngandong I (44·5), a little lower even than in the Neanderthal skull (40·4), *differing considerably from the calvarial height index of Wadjak I skull* (52). Also the cranio-cerebral index (84) of the Ngandong V skull is lower even than the average of Neanderthal skulls (86) and *certainly much lower than in the Wadjak I skull.* Dubois agrees with Oppenoorth that the Ngandong V is the most Neanderthaloid one of all *Homo soloensis* skulls. That also the Ngandong I skull contour approaches the Neanderthal skull contour appears from its superposition with the Neanderthal skull given in Oppenoorth's Fig. 6. This also shows its great difference from the Wadjak skull, whose contour nearly coincides with that of the Australian skull. Also the interglacial Riss Würm layer in which the *Javanthropus* skulls are found corresponds with the *Homo primigenius* age. Oppenoorth & Dubois (in a letter to the Dutch anthropological Bureau (16)) emphasize a resemblance of the Ngandong skulls with the Rhodesian skull, especially for the shape of the torus supraorbitalis and the nuchal plate of the occiput (in which respects relations occur still indicated in the Australian skull). Oppenoorth adds, however, that the vaulting of the frontal part of the calotte in the Ngandong skull is still less than in the Rhodesian.

The endocranial cast of the Ngandong V skull (Fig. 3), though more symmetric than the Ehringsdorf cast, shows a greater temporal bulging on the left temporal lobe than on the right.[1]

Its shape is distinctly pentagonoid. The length-breadth index of this cast is 77·1. Even if the exocranial length-breadth index (65·2 or, discounting the large torus occipitalis 67·9) is slightly too small, its difference with the endocranial index is very large. This is another expression of the fact stated by Oppenoorth and mentioned above that the cranio-cerebral index of the Ngandong V skull (83·8) is still smaller than the average of Neanderthal skulls (86 according to Weinert) and even approaches this index in *Sinanthropus* (83·6).

Also in its general shape this endocranial cast is very primitive and in some respects even approaches the much smaller and still more primitive

[1] This may be still enhanced by a thicker dural covering on the left parieto-temporal region beginning at the line indicated by three crosses on the dorsal and lateral photos. Also the dural arteries are more pronounced here than above this line and more than on the right.

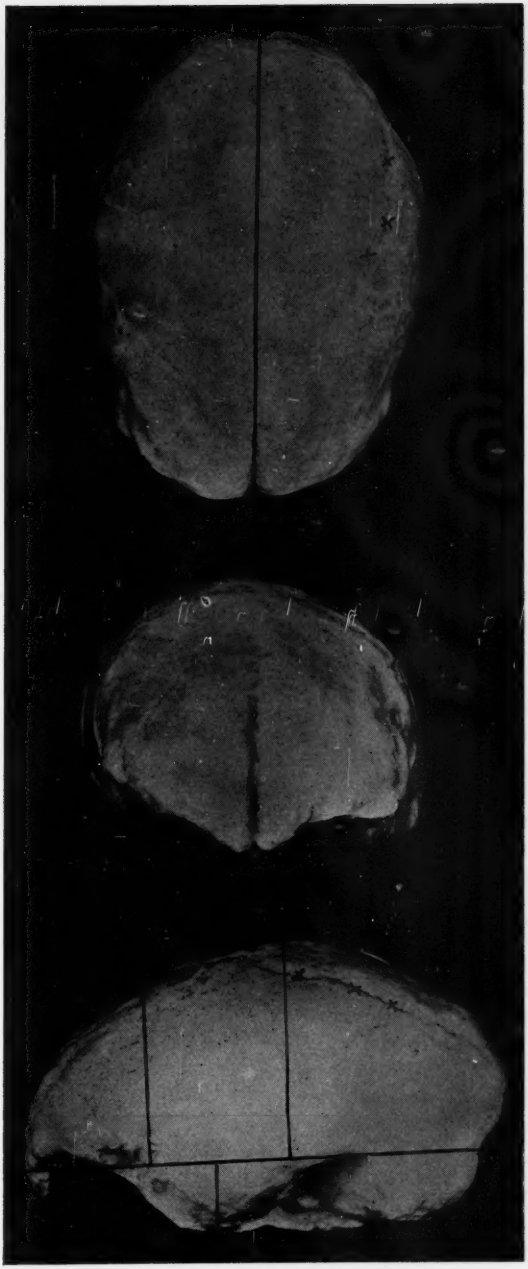


Fig. 3. *Javanthropus soloensis*, Ngandong V cast (Oppenoorth).
Lower figure 0·41 of real size.

adolescent *Sinanthropus* (E) cast (Fig. 4). So the horizontal form of both casts is distinctly pentagonoid, Ngandong V has a large rostrum that extends above the lateral horizontal as it does in *Sinanthropus* (and also in the Rhodesian). Superposing the right Ngandong V and the *Sinanthropus* cast on equal max. length and coinciding lateral horizontals, we see (Figs. 5*a* and 5*b*)[1] that, though the centro-parietal height in the Ngandong cast may be a little greater, the flattening of its frontal lobe is just as pronounced as in *Sinanthropus*, even slightly more.

It seems strange that the general height index of the Ngandong V and *Sinanthropus* "brain" are about the same, while the calvarial height index ($(22a \times 100)/2$ of Martin) over the glabello-inion line according to Black is so much lower in *Sinanthropus* (35·3) than its value in the Ngandong V (40·27) and the Neanderthal skull (40·4). Mr Oppenoorth, however, kindly called my attention to the fact that according to Black's text, p. 40, this author took the confluence of the lineae nuchae supremae as inion, whereas in the other skulls, as customary (12), the lower located confluence of the lineae nuchae superiores is taken as inion. This may also explain that[2] Black's inion lies rather high (about 29 mm.) above the endinion (and 5 mm. above the opisthokranion), while the real inion usually lies not so far in the Neanderthal skulls hitherto measured above the endinion[3] (and in the Ehringsdorf, La Quina, La Chapelle and Ngandong V skull below the opisthokranion).

Mr Oppenoorth, calculating the calvarial height index of *Sinanthropus* over what he considers the customary glabello-inion line in this subject, found it to be 39, i.e. considerably more than Black's index and only a little less than the thus calculated Ngandong V (40·27) and Neanderthal index (40·4). That the difference in our general height indices of these endocranial casts is still smaller (0·455 and 0·456 or 0·464 after reconstruction) may be due to the fact that after all our general height index is measured over the lateral horizontal, i.e. over the orbito-occipital basis, the end-point of which corresponds approximately with the endinion, not with the inion. Now the distance between the level of the endinion and that of the inion, though in Neanderthaloid skulls the endinion always is lower, shows enough variation to explain that the endocranial (so to say endinion) height index, of the skulls may approach each other still more than the exocranial or calvarial (so to say inion) height index. We should not forget that, however important the glabello-inion line is in skull comparison, the inion, being determined by the confluence of the lineae nuchae superiores, i.e. by muscle insertion, is not indicative of brain relations, for which the endinion would be of more value.

Another point in which the general shape of both casts resemble each other very much is the occipital contour (see Fig. 5). That this contour differs from that of the La Chapelle and Rhodesia cast is shown in Fig. 6. Also the length-breadth index of the endocranial casts, 77·1 of the Ngandong V and 77·09 of the *Sinanthropus* cast, according to the measurement on our specimen are about the same. The estimated volume of the Ngandong V skull, 1300 c.c., is a good deal larger than that of the *Sinanthropus* E skull (980 according to

[1] The contour of the right hemisphere of *Sinanthropus* is made by Dubois (5).

[2] Black himself emphasizes that the inion is difficult to determine on account of some erosion of the externis occipital surface.

[3] Spy I 10, Spy II 15, Ehringsdorf 18. In recent skulls (with the exception of the Australian) the inion usually lies somewhat below the end inion, or (less frequently) on the same level (Martin).

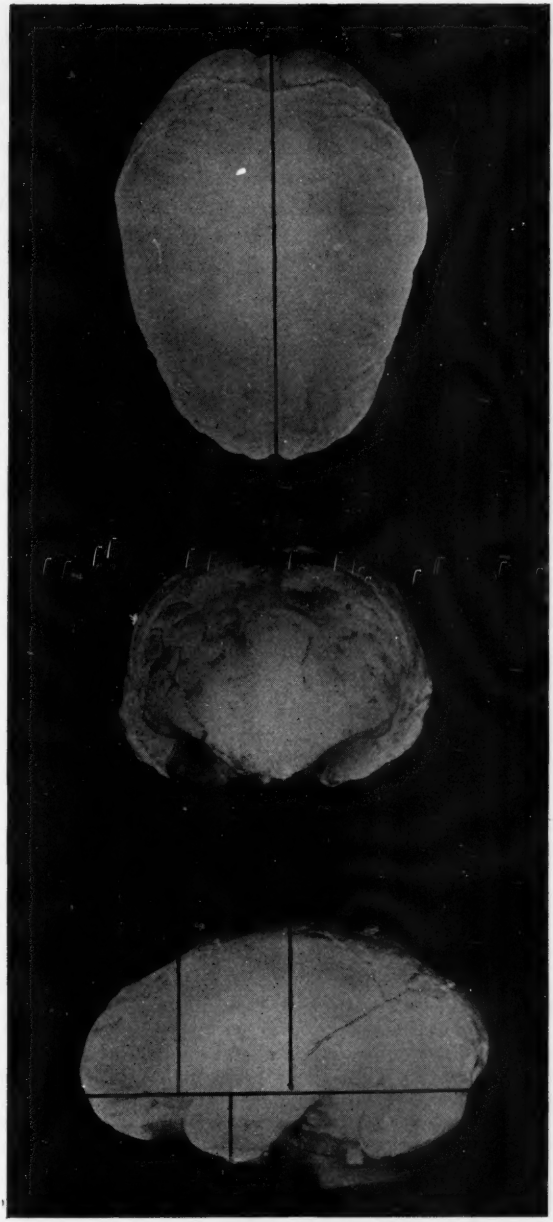


Fig. 4. *Sinanthropus pekinensis* cast (E) (Davidson Black).
Lower figure 0·41 of real size.

Black).[1] We should however keep in mind that *Sinanthropus* E is an adolescent female, while Ngandong V is an adult male. The capacity of the later discovered male *Sinanthropus* D, according to Black's measurements and contours, is substantially in excess of 1000 c.c.

Also the fact that the cranio-cerebral index, calculated with the corrected external length of 21·2 (above the torus occipitalis) in Ngandong V (84·0) differs so little from that in *Sinanthropus* (83·6) shows its primitive position (Oppenoorth).

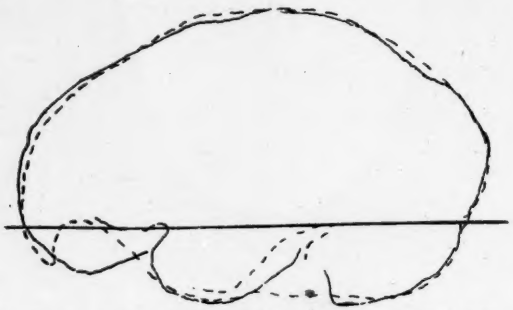


Fig. 5*a*. Continuous line, left hemisphere, *Sinanthropus*; dotted line, left hemisphere, Ngandong V endocranial cast.

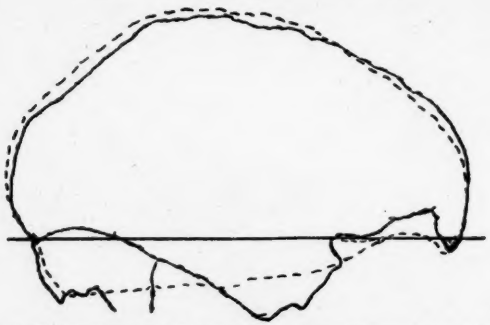


Fig. 5*b*. Continuous line, right hemisphere, *Sinanthropus*; dotted line, right hemisphere, Ngandong V endocranial cast.

Although this index is about the same in *Pithecanthropus* (83·7), the other features of *Pithecanthropus* differ considerably from either the *Sinanthropus* and *Javanthropus Soloensis*. Moreover the frontal fissuration of *Pithecanthropus* is distinctly chimpansoid (Kappers (9)). Although the impressions occurring on the left hemisphere on the Ngandong V cast are not sufficiently complete, the traces of the midfrontal (our 7) and inferior frontal (4) on the left hemisphere as well as all other features are distinctly human. Also the frontal fissures of *Sinanthropus* are prevailingly human ((8) and (19)).

[1] Black even supposed that after final reconstruction its capacity may prove to be more than 1000 c.c. The capacity of the female Ngandong I skull, calculated after outside measurements with Welcker's method I, is 1140 c.c., with Manouvrier's method 1215 c.c. (Oppenoorth (14), p.111)

On the other hand, there are distinct differences between the *Sinanthropus* and Ngandong V cast.

The smaller size of the *Sinanthropus* cast cannot be accounted for only by its younger age (supposed to be about 15 years). Other differences are: far more pointed frontal lobe in *Sinanthropus*, correlated with its small orbital breadth, the lateral orbital protrusion so pronounced in Ngandong V, as seen from above (Fig. 4), being very small in *Sinanthropus*. This also causes the transition of the frontal lobe to the rostrum in *Sinanthropus*, as seen from the front, to be much more gradual than in Ngandong V. Especially the fact emphasized by Shellshear & Elliot Smith (19) that the occipital lobe bulges out behind the lambda suture gives the *Sinanthropus* "brain" a far more primitive character.

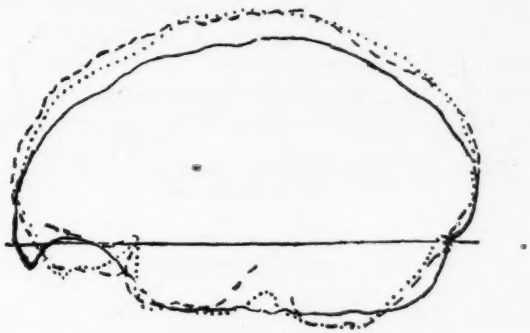


Fig. 6. Continuous line, Ngandong V; broken line, Rhodesian; dotted line, La Chapelle endocranial cast.

As to which of the Neanderthaloid skulls comes nearest to the *Javanthropus soloensis* skulls, this question is answered by Oppenoorth for the Ngandong I skull on which he superimposes in his Fig. 6 the external contour of the Neanderthal skull which resembles the Ngandong I very much, more even than the external contours of the La Chapelle and Rhodesian skulls which Vallois (21) gives together with the Ngandong I, showing the more primitive relations of the latter.[1]

Similarly the contours of the endocranial casts of La Chapelle and Rhodesian skulls superimposed upon the Ngandong V endocranial cast with coinciding lateral horizontals and making them on equal maximum lengths, show the more primitive shape of the Ngandong V cast whose Neanderthaloid character seems beyond doubt.

[1] According to Oppenoorth's data, the features of the Ngandong I skull are somewhat less primitive than those of Ngandong V, but this may be due to the female sex of the Ngandong I whose length-breadth index is 72·3?, calvarial height index 44·5?, glabello-bregma angle 45·5° and craniocerebral index 86.

POSTSCRIPT

When the manuscript of this paper was ready Mr Oppenoorth kindly sent me the endocranial casts of his *Homo soloensis* (Ngandong) IV and I. Of the Ngandong IV calotte the occipital bone is failing, the calvarium ending with the lambda suture. Besides, the whole basis, including the basal surface of the orbital protrusion, fails. The dorsal part, however, is complete and the endocranial cast of it very beautiful. The absence of the occipital and cerebellar parts and the incomplete orbital parts do not allow me to draw the

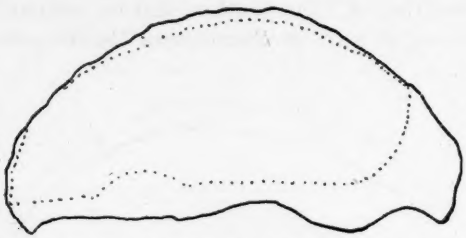


Fig. 7*a*. Left hemisphere, Ngandong IV (dotted line) superposed on Neanderthal cast.

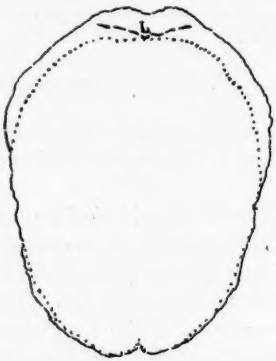


Fig. 7*b*. Ngandong IV (dotted line) Neanderthal cast. *L* = top of the lambda suture.

lateral horizontal and calculate its general height index. I therefore compared this endocranial cast with that of the Düsseldorf Neanderthal skull, the external contour of which shows a great resemblance with the Ngandong I external contour according to Mr Oppenoorth.

For this purpose I made a contour of the endocranial Neanderthal cast, adding in the same figures (7) the contour of the Ngandong IV making the fronto-lambda distance equal (they do not differ very much, this distance in the Neanderthal cast being 15·95, in the Ngandong IV 15·41). Superimposing

the frontal and the lambdoid points of the contours it appears also that the brain of this *Homo soloensis* specimen is lower than this Neanderthal cast, (Fig. 7 *a*) thus proving again its primitive shape. The superimposition of the dorsal contours (Fig. 7 *b*) shows that this brain is also less broad than the Neanderthal brain.

Concerning the endocranial cast of Ngandong I, I shall not say much, as this skull will be described by our colleague, E. Dubois. I may, however, remark that though this "brain" is certainly higher than the other in the central region (general height index 0·484?),[1] the sloping down of the frontal area is equally striking as in the other casts. Besides this cast—as far as it allows an opinion on this point—seems to have a small frontal width.

Taking all together, there seems no doubt that of all the endocranial casts hitherto available, the *Homo soloensis* group belongs to the most primitive, approaching in some respects the *Sinanthropus* endocranial cast.

In connexion herewith I may add that, according to Oppenoorth, the implements found with the Ngandong skulls are partly the same as those found with the *Sinanthropus* skulls(15). To this, however, we should not give too much value, since the horn and bone implements referred to have been in use later, especially in Europe, where they even only appeared in later periods.

REFERENCES

(1) Anthony (1913). "L'encéphale de l'homme fossile de la Quina." *Bull. Soc. Anthrop. Paris*, 6e sér., t. IV, p. 117.

(2) Black, D. D. (1931). "On the adolescent skull of *Sinanthropus pekinensis* in comparison with an adult skull of the same species and with other hominid skulls, recent and fossil." *Paleont. sinica*, D, vol. VII, fasc. II. Peking.

(3) Boule (1921). *Les hommes fossiles*, p. 146. Paris.

(4) Boule & Anthony (1911). "L'encéphale et l'homme fossile de la Chapelle aux Saints." *Anthropologie*, Paris, t. XXII, p. 129. See also Boule (1911). "L'homme fossile de la Chapelle aux Saints." *Ann. Paléont.*

(5) Dubois (1933). "The shape and size of the brain of *Sinanthropus* and *Pithecanthropus*." *Proc. K. Akad. Wet. Amst.* Bd. XXXVI, S. 145.

(6) Harris, H. A. (1926). "Endocranial form of gorilla skulls." *Amer. J. phys. Anthrop.* vol. IX.

(7) Hrdlicka (1930). *The Skeletal Remains of Early Man*, p. 230. Washington.

(8) Kappers, C. U. Ariëns (1933). "The fissuration of the frontal lobe of *Sinanthropus pekinensis* Black compared with the fissuration in Neanderthal men." *Proc. K. Akad. Wet. Amst.* Bd. XXXIV.

(9) —— (1929). "The fissures on the frontal lobe of *Pithecanthropus erectus* Dubois compared with those of Neanderthal men, Homo recens and chimpanzee." *Proc. K. Akad. Wet. Amst.* Bd. XXXII, S. 182. See also Ferrier lecture: "On some correlations of brain and skull." *Philos. Trans.* (1932), B, vol. CCXXI, p. 391.

(10) Keenan (1934). "Correlation of certain cranial indices with those of the brain." *Psychiat. neurol. Bl.*, Amst., p. 635.

(11) Keith (1929). *The Antiquity of Man*, vol. I, p. 331. London.

[1] The Ngandong V height index is at best 0·464. This agrees with the fact that the calvarial height index in Ngandong V is 40·27 in Ngandong I 44·5.

(12) MARTIN, H. (1914). *Lehrbuch der Anthropologie*, p. 737.
(13) —— (1923). *L'homme fossile de La Quina*. Paris: Doin.
(14) OPPENOORTH (1932). *Wet. Meded. Dienst. Mijnb. Ned.-O.-Ind.* No. 20. For his preliminary description of the Ngandong IV and V skull see: OPPENOORTH (1932). "De vondst van paleolithische menschelijke schedels op Java." *Mijningenieur*, No. 6, p. 106, with English summary. See also: OPPENOORTH (1932). "Ein neuer diluvialer Mensch von Java." *Natur. u. Mus.* vol. LXII, p. 269.
(15) —— (1936). "Een prehistorische cultuur centrum langs de Solorivier." *Tijdschr. Ned. Aardrijksk. Genoot.* d. LIII, p. 399 (see specially p. 409).
(16) (OPPENOORTH &) DUBOIS (1936). *Mensch en Maatschappij*, Juli, p. 303.
(17) SCHWALBE (1906). *Z. Morph. Anthr.*, Sonderheft.
(18) —— (1914). "Über einen bei Ehringsdorf in der Nähe von Weimar gefundene Unterkiefer des *Homo primigenius*." *Anat. Anz.* Bd. XLVII, S. 337.
(19) SHELLSHEAR, J. L. & SMITH, G. ELLIOT (1934). "A comparative study of the endocranial cast of *Sinanthropus*." *Philos. Trans.* B, vol. CCXXIII, p. 469.
(20) SMITH, ELLIOT (1926). "Casts obtained from the brain of fossil men." *Natural History*, vol. XXVI, No. 3, pp. 294–9.
(21) VALLOIS, H. (1935). "Le *Javanthropus*." *Anthropologie*, Paris, t. XLV, p. 71.
(22) VIRCHOW, H. (1920). *Die menschlichen Skelettreste aus dem Kämpfeschen Bruch im Travertin von Ehringsdorf bei Weimar*. Jena: Fischer.
(23) WAGNER (1935). "Endocranial diameters and indices etc." *Biometrika*, vol. XXVII, p. 88.
(24) WEIDENREICH, F. (1928). *Der Schädelfund von Weimar-Ehringsdorf*, bearbeitet von Wiegers, Weidenreich und Schuster. Jena: Fischer. See also his paper in *Natur. u. Mus.* (1928), No. 13.
(25) WEINERT (1922). "Neue untersuchungen über die Calotte des *Pithecanthropus erectus*." *Z. Ethn.* S. 199.

ON THE EXISTENCE OF ABDOMINAL VAGAL PARAGANGLIA IN THE ADULT MOUSE[1]

By N. GOORMAGHTIGH

From the Department of Pathology, University of Ghent (Belgium)

CONTENTS

		PAGE
I.	Introduction	77
II.	Technique	78
III.	The chromaffin paraganglionic cells in the adult mouse	78
IV.	The abdominal vagal paraganglia	79
V.	The influence of suprarenalectomy	84
VI.	Discussion	84
VII.	Summary	87
	References	88
	Explanation of Plates I and II	89

I. INTRODUCTION

We owe to Kohn (18, 19, 20) the conception of the paraganglionic tissue (abbrev. p.g. tissue). The latter originates from the neural crest at the same time as the ganglionic elements (12) and remains in close contact with the ganglia and nerves of the autonomic nervous system (11, 12, 13). For a long time the distinctive feature of this p.g. tissue was considered to be its chromaffinity, i.e. the peculiar property of its constituent cells to stain yellow after bichromate fixation.

In recent years, however, following the controversy about the true nature of the carotid body—also a paraganglion according to Kohn (20, 21)—it was suggested that this histo-chemical reaction was not the distinguishing feature of every paraganglion. To use the words of de Winiwarter (37), "the presence or absence of a chromaffin reaction is not a criterion for or against the paraganglionic nature of these elements but only a way to determine their function".

At present, Kohn (21) and his co-workers (29, 31, 38) recognize two types of paraganglia: (1) the chromaffin paraganglia associated with the (ortho) sympathetic and similar to, if not identical with, the suprarenal medulla; (2) the paraganglia devoid of chromaffinity and always found in close connexion with nervous plexuses composed of cranial nerves and sympathetic fibres.

In their opinion, the carotid body and the *paraganglion supra cardiale* (Penitschka (31)) belong to the latter group. Terni (33, 34) and Muratori (26, 27). hold a similar conception. However, their view is not shared by everyone.

[1] A preliminary note to this paper has been published in *C.R. Soc. Biol.*, Paris, 1935, t. CXX, p. 1348.

De Castro (8, 9) stands as a firm opponent to the opinion of Kohn, Terni and their collaborators. Nonidez (28) is also very cautious in the interpretation of these interesting organs. In my opinion the matter can only be settled by new and extensive contributions to the embryology of the carotid body and of the corresponding structures situated in the vicinity of the aorta. In a recent paper (14) I have expressed the opinion that the comparison between the embryological observations of Benoit (1) on the first stages of the carotid body and my own (11, 12) on the origin of the paraganglionic tissue of the solar plexus, tends to support the opinion of Kohn, Terni and de Winiwarter. Moreover, Benoit's work aims to prove that the carotid body is in the first place dependent on the vagus for its formation.

If this conclusion is correct, it may be said that the sensory nerves corresponding to the vaso-sensitive zones of the carotid and the aorta are each provided with a non-chromaffin paraganglion.

In this paper, I intend to give evidence in favour of a new conception, namely, that of the existence of non-chromaffin paraganglia associated with the abdominal vagi.

II. TECHNIQUE

Since the main point of my demonstration centres round the histochemical properties of definite cell groups, some technical details may be useful. Our investigations were carried out on the normal and on the bilaterally adrenalectomized adult mouse. The animal was killed by carbon monoxide. After removal of the skin the partly eviscerated abdominal cavity was fixed in Zenker-Formol solution for 6 hours and in potassium bichromate (3 per cent) for 24 hours. Imbedding took place in paraffin (56° C.) after prolonged immersion in 70 per cent alcohol plus a few drops of tincture of iodine. Frontal serial sections of the posterior half of the abdomen extending from the diaphragm to the pelvic organs were stained either by haemalum or by haemalum, acid fuchsin and lichtgrün (variation of Masson's method) or by Mallory's phosphotungstic haematoxylin.

III. THE CHROMAFFIN PARAGANGLIONIC CELLS IN THE ADULT MOUSE

Before approaching the main theme of this paper we have found it necessary to resume briefly what is, in our view, the behaviour of the chromaffin paraganglionic tissue in the adult mouse.

It has always been Kohn's (20, 21) opinion that the paraganglionic chromaffin tissue of mammals reached the height of its development at birth. At this time it is represented in the retroperitoneal region by a compact organ placed caudad to the superior mesenteric artery.

This bulky paraganglion has vanished in the adult, but our methodical survey, of which the chief data were published in 1928 (13), has shown that the disappearance of this solid foetal paraganglion is the result of a scattering process of its constituents. The process is already very marked on the first week after birth. The p.g. elements migrate in a cranio-caudal direction along the

nerves of the mesenteric plexuses as far as the utero-vaginal or deferentio-prostatic ganglia.

In the site of the original anlage, only a thin interrupted string of paraganglionic cells remains in contact with the wall of the left renal vein close to the point where it enters the inferior vena cava. In fact, in this particular region, these minute cell groups lie between the walls of these vessels and the retroperitoneal fat lobules. These cells generally adhere to nerve fibres or to a small ganglion. However, in the vicinity of the left renal vein a small number of cells lies at a greater distance from the nervous structures, but in this instance vascular connexions between ganglion and the paraganglionic cells can be readily demonstrated. In the rest of the retroperitoneal area in question, the connexions between the nervous and glandular structures are close. The cell constituents of the latter are either adherent to the nerves and ganglia or imbedded in them. They are exceptionally abundant in the utero-vaginal or deferentio-prostatic ganglia, a fact in agreement with earlier observations of Blotevogel (2) and Watzka & Penitschka (38).

In view of what I have to say about the main theme of this paper, I want to emphasize the following points: (1) With the exception of a few chromaffin cells embedded in the solar ganglia, the bulk of chromaffin tissue lies caudally to these ganglia. Among these yellow stained cells, a colourless pale cell is occasionally found. Stoerk & v. Haberer have proved long ago that the glandular cycle of this type of cell involves an initial non-chromaffin stage. The progressive loading of chromaffin granules can be clearly followed in the cell groups under consideration. Even small vacuoles appear in the fully loaded cells. This tends to prove that they possess a glandular function as Grynfelt (15) was actually the first to suggest. (2) A second feature of importance is that the cells vary greatly in size. The unstained cells are small; the stained ones can attain the same size as the suprarenal medulla cells. This is especially true for the p.g. cells imbedded in the ganglia located near the prostate or uterus. The volume of the largest cuboidal p.g. cells reaches $3375\,\mu^3$. The average volume of one cell calculated on fifty measurements is $1572\,\mu^3$. The size of the nuclei is not uniform (average size $5{\cdot}5\,\mu$). (3) A third feature of importance consists in the fact that these chromaffin p.g. cells come under observation as isolated elements or very small cell groups of five cell units at a maximum.

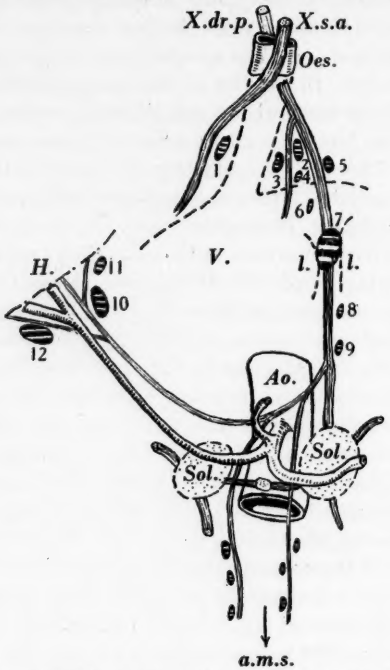
IV. THE ABDOMINAL VAGAL PARAGANGLIA

Distribution. In the thorax, the right vagus nerve of the adult mouse lies dorsally to the oesophagus (*Oes.*, Text-fig. 1) and keeps in close contact with its wall for a short distance in the abdominal cavity itself (*X.dr.p.*, Text-fig. 1). When a thin bundle has branched off towards the posterior wall of the stomach (*V.*, Text-fig. 1), the main trunk of the right vagus nerve leaves the oesophagus and runs towards the origin of the coeliac artery where it splits up into several branches: one accompanying the hepatic artery, one running into the solar plexus (*Sol.*, Text-fig. 1 and *X.dr.p.*, Pl. I, fig. 1) and two others running parallel

to the aorta in the direction of the origin of the superior mesenteric artery (*a.m.s.*, Text-fig. 1).

The left vagus (*X.s.a.*, Text-fig. 1 and *X.s.a.*, Pl. I, fig. 2) lies ventral to the oesophagus and its branches are distributed chiefly over the anterior stomach wall.

We have traced *twelve* distinct paraganglia along the vagus branches between the diaphragm and the origin of the coeliac trunk (Text-fig. 1): (1) one



Text-fig. 1. Schematic representation of the abdominal vagi and the non-chromaffin paraganglia (horizontally striped bodies). *Ao.* aorta; *a.m.s.* superior mesenteric artery; *l.l.* lymph nodes; *H.* liver; *Oes.* oesophagus; *V.* stomach; *X.dr.p.* right posterior vagus; *X.s.a.* left posterior vagus. The paraganglia are numbered and some of them are shown by the microphotographs.

paraganglion (1, Text-fig. 1; *p.g.* 1, Pl. I, figs. 2 and 4) is connected with the anterior vagus running along the oesophagus; (2) close to the right vagus come to notice: (*a*) one paraganglion at the place where a posterior gastric nerve bundle branches off (2, Text-fig. 1 and *p.g.* 2, Pl. II, fig. 6); (*b*) two p.g. along this small branch (3, 4, Text-fig. 1 and *p.g.* 4, Pl. I, fig. 5); (*c*) five along the main trunk as far back as the origin of the coeliac artery (5, 6, 7, 8, 9, Text-fig. 1); (*d*) one large paraganglion and two smaller ones distributed among the dividing branches of an hepatic vagus branch (10, 11, 12, Text-fig. 1). The

exact location of one of the paraganglia in the hilus region of the liver is shown on Pl. II, fig. 8. In *p.g.* 10, close to the portal vein (*p.v.*), the wall of which is slightly disrupted in the preparation, a paraganglionic cell group can be distinctly seen. With a higher magnification the relation between this paraganglion and nerve bundles (*n.*), venules (*v.*) and lymph-ducts (*ly.*) is illustrated (*p.g.* 10, *v.*, *n.*, *ly.*, Pl. II, figs. 9, 10). We think that the accumulation of p.g. tissue in the hilus of the liver is of physiological importance; it will be interesting to explore, in the future, the hilus of other organs.

Caudad to the coeliac artery exist several smaller non-chromaffin paraganglia. They are adherent to the nerve bundles running towards the origin of the superior mesenteric artery (*a.m.s.*, Text-fig. 1). From these nerve bundles branch off small nerves for the pancreas. Along one of them lies the paraganglion represented in Pl. II, fig. 7. The superior mesenteric artery is on the left, the pancreas on the right of the photomicrograph. The paraganglion (*p.g.*, Pl. II, fig. 7) and its corresponding nerve (*n.*, Pl. II, fig. 7) are cut longitudinally.

This distribution scheme is very constant in five specimens. The two largest paraganglia are found respectively in the hilus of the liver (*p.g.*, Pl. II, figs. 9, 10), and in the main trunk of the right vagus at a point where the latter enters a groove between two lymph nodes which are a constant anatomical feature of the retroperitoneal region in the adult mouse (*l.l.*, Text-fig. 1 and Pl. I, fig. 1). The count of the vagal paraganglia is probably incomplete, since our series of sections does not extend over the whole anterior stomach wall. However, all the abdominal branches of the vagi we have examined so far are provided with satellite paraganglionic material. The fact that this tissue is unevenly distributed along these branches, and that the largest paraganglia are always located at the same place, allows us to assume that the amount of this p.g. tissue is proportionate to the extent of the area innervated by each particular branch. The abundance of this p.g. tissue in the hilus of the liver is suggestive in this respect. We feel that minute researches in this direction may lead to a clearer understanding of these bodies.

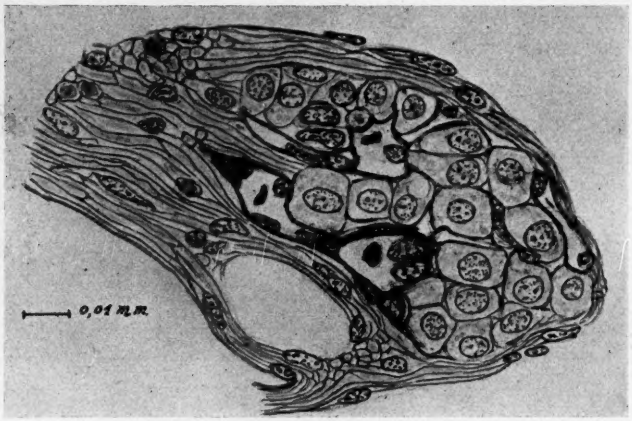
These structures are undoubtedly of paraganglionic nature: the distinctive, dusty appearance of the nuclear chromatin, the architecture of the cell trabeculae (Text-fig. 2), the mode of vascularization and the behaviour of the capillaries with their large endothelial cells and especially the close connexion of the cells with nerve fibrils, are specially characteristic features. They answer to the classical description given by Kohn, Grynfelt (15), Swale Vincent (36) and others.

That these glandular cell groups with a definite endocrine appearance are aberrant cortical tissue is out of the question, since the latter never occurs in the medial line of the body. Moreover, aberrant cortical nodules are always spherical; their cells are larger; the chromatin presents a coarse aspect; while the protoplasm is dense or distinctly vacuolar. Finally they are not in close relation with nerve trunks.

It could be suggested also that these intra- or juxtaneural structures represent aberrant islets of Langerhans. The latter also are known to be in close

contact with microganglia in the embryo (Van Campenhout(35)). However, their morphology bears no resemblance to the glandular bodies associated with the vagus branches: the type of vascularization is quite different.

Morphological characteristics of vagal paraganglia. The distinctive feature of these vagal paraganglia consists in the absence of the chromaffin reaction which belongs to the true sympathetic paraganglia. I am aware that this proposition is, at first sight, open to criticism. The success of this colorimetric test depends, indeed, on adequate fixation and the lack of chromaffinity could



Text-fig. 2. Non-chromaffin paraganglion imbedded in the right abdominal vagus nerve. The capillaries run throughout the paraganglion between the nerve fibrils. Adult mouse 281,233, slide 192.

be possibly the result of a faulty technique. (1) Our observations are made, however, on large frontal sections, and since the chromaffin reaction was positive on the same slide, in the p.g. cells lying caudad to the superior mesenteric artery, a faulty technique could not explain the different colorimetric behaviour of the vagal paraganglia. (2) Other features enable a distinction to be drawn between vagal and true sympathetic paraganglia. While in the adult mouse the latter present an extremely scattered arrangement, the vagal paraganglia form solid, compact, ellipsoidal structures of a comparatively large size. The largest among them are distinctly lobulated (*p.g.* 7, Pl. I, fig. 3, and *p.g.* 10, Pl. II, fig. 8) and measure respectively $0{\cdot}18 \times 0{\cdot}06 \times 0{\cdot}06$ mm. and $0{\cdot}20 \times 0{\cdot}15 \times 0{\cdot}06$ mm. (liver hilus), while the smallest measure $0{\cdot}05 \times 0{\cdot}06 \times 0{\cdot}05$ mm. It may be interesting to note that after fixation the right vagus of the adult mouse at a point where it passes through the diaphragm is approximately 0·13 mm. thick (*X.dr.p.*, Pl. II, fig. 6). This gives an idea of the relation of size between the paraganglia and the nerve trunks with which they are associated and gives a hint as to the possible dimensions of the same structures in larger

mammals. (3) The cells have a more uniform size than those of the corresponding sympathetic paraganglia and are generally of prismatic shape. (4) There is also more uniformity in the size of the nuclei; the chromatin network, though very delicate (Text-fig. 2 and *p.g.* 7, Pl. I, fig. 3), stains more deeply. The average size of the nuclei is 5·7 μ, while that of nuclei of the sympathetic p.g. cells averages 5·5 μ. (5) The relation to nerve trunks is even closer than that of the sympathetic paraganglia. They are nearly always imbedded in the nerve trunk (Text-fig. 2 and Pl. I, figs. 3, 4). Several venules run out from the paraganglion into the nerve (Text-fig. 2) or form a network round it. If a hormone is produced by these structures, it unavoidably permeates the surrounding nerve fibrils. This is particularly evident in Text-fig. 2, which shows how close is the contact with the capillaries and how the presence of delicate vacuoles (also seen in Pl. II, fig. 7) speaks in favour of a glandular function of the cells. This drawing shows also that the blood of the capillary network flows out into larger peripheral sinuses which are on the other hand in communication with distended capillaries running between the nerve fibrils.

It is an open question whether the close connexion with the lymphoid tissue is of biological significance. In this respect we point to the fact that in the vicinity of the paraganglia of the hilus region of the liver a small lymphnode is regularly found (*l.*, Pl. II, fig. 8).

In the largest paraganglia two or three small ganglionic cells are present. The other vagal paraganglia are devoid of them.

The vagal paraganglia of the heart. The comparatively simple mode of nerve distribution in the cranial retroperitoneal region of the mouse offers ideal conditions for the conclusive demonstration of the existence of vagal (parasympathetic) paraganglia. Aware of this new fact, we have investigated other anatomical regions. In a recent preliminary paper, one of my co-workers, R. Pannier (30), has made a survey of the epicardial ganglia of the adult cat. In this region, as Woollard (40) has pointed out, it is impossible, at present, to distinguish the sympathetic from the vagal constituents. The two are intermingled. On this material, however, Pannier has been able to demonstrate two important facts: (1) every epicardial ganglion is provided with a satellite microparaganglion; (2) these paraganglia are generally of a mixed nature (either predominantly chromaffin or predominantly non-chromaffin). He found, however, one entirely non-chromaffin paraganglion lying on the dorsal side of the bifurcation of the pulmonary artery and quite distinct from the supracardial Penitschka body.

We have consequently every reason to believe that the two types of nerves concerned with the innervation of the heart are each of them provided with a distinct glandular paraganglionic annex. R. Panner will soon give full particulars of his observations.

V. THE INFLUENCE OF SUPRARENALECTOMY

As is well known, when performed in two stages double adrenalectomy is not fatal in the mouse, thanks to the hypertrophy of aberrant cortical tissue. The behaviour of the chromaffin sympathetic paraganglionic tissue in those animals does not differ from the controls. We cannot demonstrate any compensatory hypertrophy. The only possible difference may be this: the proportion of fully loaded chromaffin cells appears to be larger but one cannot draw conclusions from such unconvincing cytological changes.

As to the abdominal vagal paraganglia there is no striking change from the controls.

VI. DISCUSSION

(1) We feel entitled to draw our conclusions as to the vagal nature of these paraganglia from their close association with the vagus nerve. It must be borne in mind, however, that, according to modern research, the vagus nerve has not a homogeneous structure in many mammals. Kiss & Michalik (22) go so far as to say that the abdominal vagus in man contains only 20 per cent of true vagal fibres, the greater part being of sympathetic nature. But the views of these observers are still a matter of controversy. Kuntz (discussion (24)) points out that this conception differs radically from the classical view, and Ranson *et al.* (32) strongly oppose most of the conclusions of Kiss's work. The physiologists, however, favour the idea of the complex structure of the vagus. How the matter stands in the mouse is not known. But since the histochemical features of the paraganglia under discussion are so decisively distinct from those associated with the sympathetic nerves, it can be safely assumed that they are functionally related to the true vagal components of the vagus.

It may be that in mammals where sympathetic fibres in the abdominal vagus are very numerous (cat), the paraganglia under consideration are heterogeneous (i.e. composed of chromaffin and non-chromaffin constituents).

(2) The distinction between chromaffin, ortho-sympathetic paraganglia and non-chromaffin, vagal paraganglia in the adult mammal is a new concept. In the embryo, however, de Winiwarter (37) has recently drawn attention to the presence of paraganglionic cells in the cervical vagus. In the cervical sympathetic chain of a 35 days old cat embryo, he describes paraganglionic cell groups. He notices similar cells in the cervical vagus. The latter are even more conspicuous since they offer a better contrast with the more differentiated vagal ganglionic cells. Although the author admits that the function of p.g. cells may depend upon the type of nerve they are related to, he does not definitely refer to a distinction between sympathetic and vagal paraganglia. At this stage of development colorimetric tests cannot be applied.

According to de Winiwarter, these cells could also be satellites of sympathetic fibres present in the vagus. Whatever is the correct interpretation of these observations, the fact remains that p.g. cells are present in the vagus of the

embryo. Through a process of migration they could furnish the material of the adult abdominal vagal paraganglia.

On the other hand, we must mention the important contributions of G. Muratori (26, 27) who has studied the innervation of the carotid body in birds; he described, already in 1932, the existence of non-chromaffin paraganglionic tissue in the cervical vagus and inside the nodose ganglion (intravagal paraganglia). According to him, this tissue has the same signification as that of the carotid body: both have in common a sensory vagal innervation. The observations of Muratori and of de Winiwarter support our own in the adult mouse, but they confront us with a new difficulty which we are not able to solve definitely: are the abdominal vagal paraganglia, described in this paper, connected with sensory or motor constituents of the abdominal vagus?

The paraganglia discovered by Muratori are situated in the vicinity of a body which according to recent physiological investigation (C. Heymans (16)) has a sensory function; this body is, moreover, closely related to the carotid vaso-sensory area. To the corresponding aortic sensory area is related the Penitschka organ or paraganglion.

Recently, C. Heymans and his co-workers (17) admit the existence of accessory vaso-sensory areas, in branches of the coeliac and mesenteric arteries.

Do the abdominal vagal paraganglia stand in the same physiological relation to these accessory areas as the carotid and supracardial bodies do towards the two principal vasosensory areas? No evidence exists in favour of this conception, since Heymans points out that the reflexes originating from these accessory areas are maintained when the cervical spinal cord is sectioned. This observation shows that these reflexes do not use, at least exclusively, the pathway of the vagi to which the paraganglia we have described are so closely related. In other words no evidence is available at present in favour of the idea that the abdominal vagal-paraganglionic complexes have the same physiological signification as the vagal-paraganglionic complexes of the aortic and carotid regions.

We must point also to the fact that according to the actual available data (22), the afferent fibres of the vagus are in all probability more abundant in the cervical and thoracic than in the abdominal region. In contrast to this, in the adult mouse, the vagal paraganglionic tissue of the abdomen is more abundant than the p.g. tissue of the carotid and supracardial bodies.

We conclude that, at present, no evidence of the sensory nature of the abdominal vagal paraganglia is forthcoming. We have more reason to believe that these paraganglia are a glandular annex to the efferent fibres of the vagus, since their mode of distribution and their anatomical relation to the nerve bundles are practically similar to those of the chromaffin sympathetic paraganglia which are undoubtedly in connexion with efferent fibres.

(3) If the abdominal vagal paraganglia are functionally related to the efferent fibres of the vagus, we must attempt to know the nature of the chemical substance secreted by these structures. The morphologist cannot

solve this problem. When discovered in larger mammals, it will be possible to submit them to pharmacological tests. Here lies, in our opinion, a promising field of investigation. Pharmacology may greatly help to establish the true physiological signification of the paraganglia.

In the meantime we can reason as follows: Cannon & Bacq (3), Cannon & Rosenblueth (4), confirming an earlier hypothesis of Elliott (10), have proved that the stimulation of the sympathetic fibres produces an adrenalin-like substance, if not adrenalin itself. Vagal stimulation, on the other hand, is known to release in the fluid filling the isolated heart of the frog a substance which is able to transfer the vagus inhibition to another heart (Loewi (25)). According to Loewi, this substance is in all its properties indistinguishable from acetylcholine. Recent experiments of Dale & Feldberg (7) have a very close relation to our observations. These authors reach the conclusion that stimulation of the vagi of the dog, adequate to produce a powerful contraction of the stomach wall, liberates in the venous gastric blood a substance having "all the properties of an unstable, atropine sensitive choline ester, indistinguishable from those of acetylcholine". Consequently we feel that it is reasonable to advance the hypothesis that this substance is produced by the non-chromaffin glandular structures we find precisely in or round the gastric branches of the vagi. In other words, we suggest that the non-chromaffin paraganglia associated with the vagus should contain and liberate acetylcholine. Evidence has been accumulating, in recent years, in favour of the view that adrenalin on the one hand and acetylcholine on the other transmit the motor effect of the nerve impulse from the nerve endings to the effector cell. Dale (6), to whom we owe so much valuable information on this new doctrine, affirms that all postganglionic fibres use as a chemical transmitter either adrenalin (or an adrenalin-like substance, sympathin) or acetylcholine. This duality in pharmacological phenomena seems to have, to a certain extent, its morphological counterpart in the two types of paraganglia associated with the motor fibres of the autonomic system: this is strikingly illustrated in the epicardial region of the cat where the two types of paraganglionic cells lie side by side; their close connexion corresponds to the intricate association of sympathetic and parasympathetic nerves in this region.

We want to stress again the point that the concept of the duality of p.g. tissue rests on something more than on a histochemical reaction. Other morphological features, emphasized above, separate the two types: in the mouse, the vagal paraganglia are larger than the sympathetic paraganglia, and they are in even closer relation with the nerve fibres. Is this due to the greater instability of acetylcholine which cannot withstand prolonged contact with the blood?

We insist also on the fact that the vagal paraganglia lie at some distance from the nerve endings. This observation does not stand in the way of an eventual agreement between physiological and morphological findings, since the chemical substances liberated by these paraganglia may diffuse towards

the distal end of the nerve when the latter is stimulated: the location of paraganglionic material in the hilus of the liver illustrates the fact that this tissue tends to accumulate fairly near to the point where the nerve impulse acts on the receptor cells.

Quite recently, Dale (1935 (6)) and his co-workers have come to the conclusion that a small quantity of acetylcholine is liberated when a preganglionic impulse arrives at the synapse. We are not in a position, yet, to examine how far this opinion fits in with the morphological data. We have pointed out in this paper that in one or two paraganglia of the abdominal vagus, small ganglionic cells are found. Their presence may condition the existence of a synapse and the vicinity of non-chromaffin p.g. cells shows that a liberation of acetylcholine, at this site, is possible from a morphological standpoint. But we agree that this is very scanty information. In this field of research, a closer collaboration between morphologists and experimentalists is needed. So far, the morphologists have hardly examined the sections of the autonomic nervous system submitted to pharmacological tests, while pharmacologists and physiologists have not yet explored those we have studied, with the exception of some experiments of Dale & Feldberg (7) on the gastric vagus.

After the first version of our manuscript was written, we came across the observations of Christie (5) which provide the first positive information on the presence of a vaso-depressor principle in some paraganglia: a tumour of the carotid body in man and the carotid glomus of the elasmobranchs are shown to contain a thermostable vaso-depressor principle in high concentration. Christie, who worked under the supervision of J. B. Collip, proves that this principle differs in its properties from acetylcholine—a fact which White (39) in his recent paper seems to have overlooked.

Christie's work confirms our belief that the paraganglionic system consists of three types of paraganglia: (*a*) the sympathetic paraganglia (adrenal and extra adrenal) connected with sympathetic motor fibres and secreting adrenalin; (*b*) the parasympathetic, vagal paraganglia connected with efferent fibres of the vagus and secreting a chemical substance that could be acetylcholine; (*c*) the sensory paraganglia (carotid body and supracardial body—Penitschka) connected with afferent parasympathetic fibres, embryologically a dependence of the vagus and containing a vasodepressor principle distinct from acetylcholine.

In this paper we have put forward a fact and an hypothesis. Of the fact we feel certain. As to the hypothesis, the future confrontation of physiological and morphological data will prove or disprove its soundness.

VII. SUMMARY

1. In the adult mouse the existence of abdominal vagal paraganglia distinguishable from true sympathetic paraganglia is demonstrated.

2. The vagal paraganglia are imbedded in or adherent to different branches

of the abdominal vagus. Their localization and distribution are described and illustrated.

3. Their distinctive features consist in the absence of a chromaffin reaction, in the smaller size of the cells, and in the fact that the latter are grouped in ellipsoidal compact bodies. The sympathetic paraganglia, on the other hand, have a chromaffin reaction and are scattered, chiefly caudad to the superior mesenteric artery as isolated or minute cell groups.

4. The most important accumulation of vagal paraganglionic tissue is found in the hilus of the liver and along the main branch of the right posterior vagus connected with the solar plexus.

5. Paraganglionic cell groups of the same type are present in the epicardial region of the adult cat. They form satellite bodies to the microganglia and are distinct from the Penitschka paraganglion.

6. The physiological significance of this vagal paraganglionic tissue is discussed: no proof is available that it possesses a function comparable to that of the carotid and Penitschka bodies; it is suggested that it is functionally related to the efferent fibres of the vagus nerve.

7. As to the nature of the eventual chemical substance produced by these paraganglia, the possibility of an acetylcholine secretion is put forward on the evidence provided by recent physiological research.

8. These observations offer a possible morphological way of approach to the theory of chemical transmission of the nervous impulse.

We are indebted to Prof. J. P. Hill for the interest he has taken in this work. The photomicrographs were made in his Department by Mr F. J. Pittock to whom we wish to express our thanks.

REFERENCES

(1) Benoit, A. (1928). *Arch. Biol.*, Paris, t. xxxviii, p. 220.
(2) Blotevogel, W. (1926). *Anat. Anz.*, Ergänzh. Z., Bd. lx, S. 233.
(3) Cannon, W. B. & Bacq, Z. (1931). *Amer. J. Physiol.* vol. xcvi, p. 392.
(4) Cannon, W. B. & Rosenblueth, A. (1933). *Amer. J. Physiol.* vol. civ, p. 597.
(5) Christie (1933). *Endocrinology*, vol. xvii, pp. 421 and 433.
(6) Dale, H. (1935). *Proc. roy. Soc.* vol. xxviii, p. 319.
(7) Dale, H. & Feldberg, G. W. (1933). *J. Physiol.* vol. lxxx, *Proc.* p. 16.
(8) De Castro, F. (1926). *Trab. Lab. Invest. biol. Univ. Madr.* vol. xxiv, p. 365.
(9) —— (1927). *Trab. Lab. Invest. biol. Univ. Madr.* vol. xxv.
(10) Elliott, T. R. (1904). *J. Physiol.* vol. xxxi, p. 157.
(11) Goormaghtigh, N. (1921). *Arch. Biol.*, Paris, t. xxxi, p. 83.
(12) —— (1924). *C.R. Ass. Anat.*, Strasbourg, Bd. xix, S. 149.
(13) —— (1928). *C.R. Ass. Anat.*, Prague, Bd. xxiii.
(14) —— (1935). *Bruxelles Médical*, Seizième Année, p. 38.
(15) Grynfelt, E. (1903). Thèse Fac. Médec. Montpellier, Lille.
(16) Heymans, C., Bouckaert, J. J. & Regniers, P. (1933). *Le Sinus carotidien.* Paris: O. Doin et Cie.
(17) Heymans, C., Bouckaert, J. J., Farber, S. & Hsu, F. (1936). *C.R. Soc. Biol.*, Paris, t. cxxii, p. 115.

(18) KOHN, A. (1899). *Arch. mikr. Anat.*, Bd. LIII, S. 281.
(19) —— (1900). *Arch. mikr. Anat.*, Bd. LVI, S. 81.
(20) —— (1903). *Arch. mikr. Anat.*, Bd. LXII, S. 263.
(21) —— (1929). *Endokrinologie*, Bd. V, S. 434.
(22) KISS, F. & VON MICHALIK, P. (1931). *Anat. Anz.*, Ergänzh. Z., Bd. LXXI, S. 168.
(23) KISS, F. (1933). *Ann. Anat. Path.* vol. X, p. 1078.
(24) KUNTZ, A. (1934). *The Autonomic Nervous System.* Philadelphia: Lea and Fibiger.
(25) LOEWI, O. (1921). *Pflüg. Arch. ges. Physiol.* Bd. CXCIX, S. 239.
(26) MURATORI, G. (1932). *C.R. Ass. Anat.*, Nancy, t. XXVII, p. 409.
(27) —— (1932). *Arch. ital. Anat.* vol. XXX, p. 573.
(28) NONIDEZ, J. F. (1935). *Amer. J. Anat.*, vol. LVII, p. 259.
(29) PALME, F. (1934). *Z. mikr.-anat. Forsch.* Bd. XXXVII.
(30) PANNIER, R. (1935). *C.R. Soc. Biol.*, Paris, t. CXX, p. 1350.
(31) PENITSCHKA, W. (1931). *Z. mikr.-anat. Forsch.* Bd. XXIV, S. 124.
(32) RANSON, S. W., FOLEY, O. & ALPERT, C. (1933). *Amer. J. Anat.* vol. LIII, p. 289.
(33) TERNI, T. (1924). *Arch. ital. Anat.* vol. XXI, p. 55.
(34) —— (1927). *Arch. ital. Anat.* vol. XXIV, p. 407.
(35) VAN CAMPENHOUT, E. (1935). *Arch. Biol.*, Paris, t. XXXVII, p. 122.
(36) VINCENT, SW. (1910). *Proc. roy. Soc.* vol. V, p. 82.
(37) DE WINIWARTER, H. (1934). *C.R. Ass. Anat.*, Bruxelles, t. XXIX.
(38) WATZKA, M. & PENITSCHKA, W. (1932). *Z. mikr.-anat. Forsch.* Bd. XXX, S. 29.
(39) WHITE, E. G. (1935). *Beitr. path. Anat.* Bd. XCVI, S. 177.
(40) WOOLLARD. Quoted by Kuntz.

KEY TO LETTERING

a. = arteriole.
ad. = fat tissue.
a.m.s. = superior mesenteric artery.
Ao. = aorta.
c.a. = coeliac trunk.
g.c. = ganglionic cell.
H. = liver.
l. = lymph node.
ly. = lymph vessel.
n. = nerve trunk.
Oes. = oesophagus.
Pa. = pancreas.
p.g. = non-chromaffin paraganglion.
p.v. = portal vein.
Sol. = solar plexus.
V. = *stomach.*
v. = venule.
X.dr.p. = right posterior vagus.
X.s.a. = left anterior vagus.

EXPLANATION OF PLATES I AND II

PLATE I

Fig. 1. Topographical frontal view of the cranial retroperitoneal region of an adult male mouse (frontal section). Adherent to the distal end of the oesophagus, the right posterior vagus (*X.dr.p.*) is seen in cross-section. A longitudinal section of a vagus branch runs between two lymph glands towards the solar ganglia. A paraganglion (*p.g.* 7), represented at high magnification in fig. 3, is present at the place where the nerve enters the groove separating the two lymph glands (*l.*). In (*c.a.*) a cross-section of the coeliac trunk. Mouse 101,133, slide 190, × 70.

Fig. 2. Topographical view of the same region taken from a more anterior frontal section, with the left anterior vagus nerve (*X.s.a.*) running along the oesophagus (*Oes.*) in longitudinal section. Near the lower end of this nerve is located a paraganglion (*p.g.* 1) which fig. 4 reproduces at a higher magnification. Mouse 21,933, slide 186, × 70.

Fig. 3. Non-chromaffin paraganglion (*p.g.* 7) of the right abdominal vagus nerve (*n.*), lying between two lymph nodes (*l.l.*, see Text-fig. 1). Well-stained nuclei; palisade-like arrangement of the cells. Adult male mouse 101,133, slide 190, × 640.

Fig. 4. Non-chromaffin paraganglion (*p.g.* 1) of the left abdominal vagus nerve (*X.s.a.*) with deeply stained, regular nuclei. Adult male mouse 21,933, slide 186, × 640.

Fig. 5. Ovoid-shaped paraganglion (*p.g.* 4) connected with the same branch (*n.*) (see fig. 6). Adult male mouse 21,933, slide 193, × 640.

PLATE II

Fig. 6. Non-chromaffin paraganglion (*p.g.* 2) adherent to a branch (*n.*) of the posterior right abdominal vagus (*Xd.r.p.*) and imbedded in fat tissue (*ad.*). In (*v.*) a large venule close to the paraganglion. In (*a.*) an afferent arteriole. Adult male mouse 101,133, slide 202, × 640.

Fig. 7. Longitudinal section of a non-chromaffin paraganglion (*p.g.*) close to the superior mesenteric artery and to a nerve bundle (*n.*) penetrating into the pancreas (*Pa.*). Adult male mouse 101,133, slide 158, × 640.

Fig. 8. Topographical view of the site of entry of the portal vein into the liver. In *p.g.* 10 is located a non-chromaffin paraganglion seen at higher magnification in figs. 9 and 10. Adult male mouse 21,933, slide 267, × 70.

Fig. 9. In the vicinity of the disrupted wall of the portal vein (*p.v.*) lies a non-chromaffin paraganglion (*p.g.*) in close contact with nerve bundles (*n.*). In (*a.*) a cross-section of the afferent artery; this technically imperfect section is reproduced to show a ganglionic cell (*g.c.*) among the *p.g.* cells. Mouse 21,933, slide 264, × 640.

Fig. 10. Another section of the same paraganglion (see fig. 8). (*n.*) nerve bundle; (*ly.*) lymph duct. Mouse 21,933, slide 267, × 640.

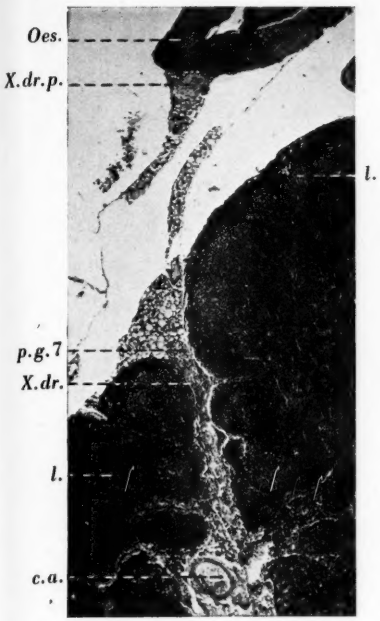


Fig. 1.

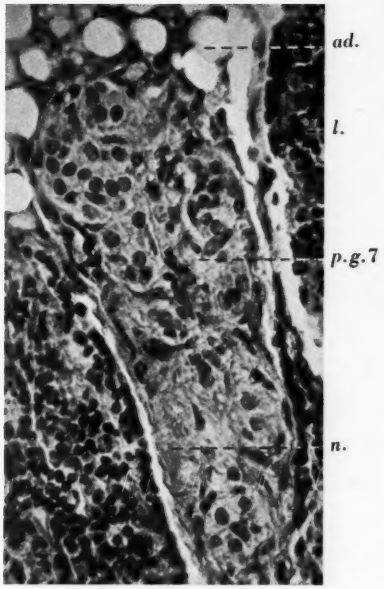


Fig. 3.

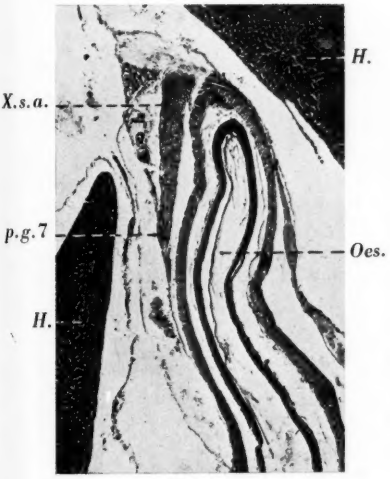


Fig. 2.

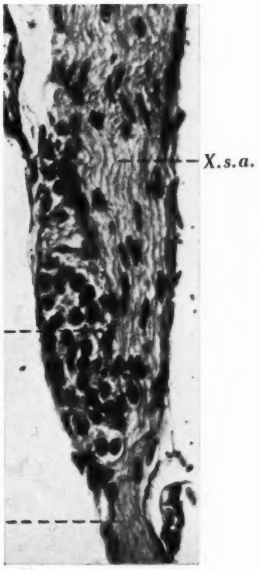


Fig. 4.

Fig. 5.

UNIV. OF MICH.

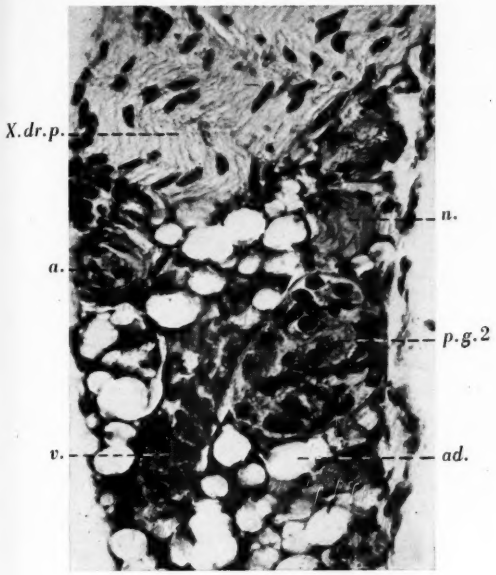


Fig. 6.

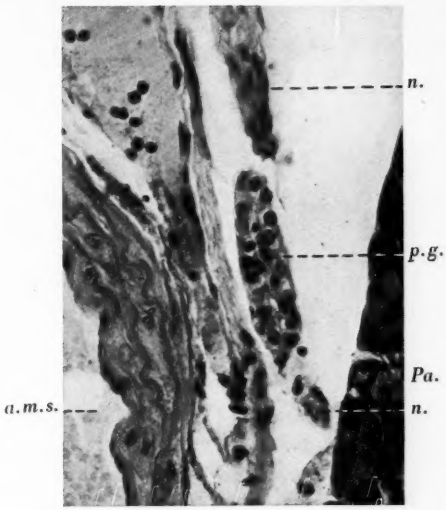


Fig. 7.

Fig. 8.

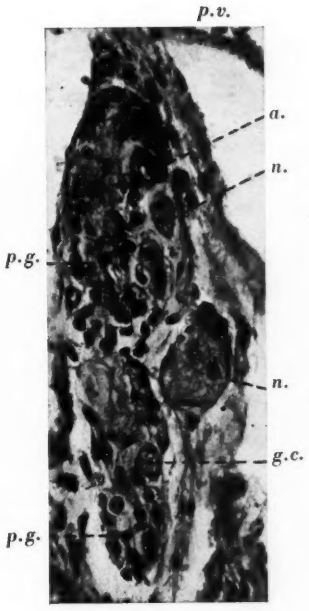


Fig. 9.

Fig. 10.

UNIV. OF MICH.

THE SECRETING AREA OF THE GLOMERULUS

By M. H. BOOK

Department of Anatomy, University of Toronto

A comparatively little-explored field in histological research has been the measurement of microscopic surfaces across which the interchange of gases, absorption of nutriment, secretion of metabolic products and the like take place. The figures for those organs of which determinations have been made are often astonishing. For example, Willson (1922) calculated that the total area of the epithelium of the adult human lung, respiratory and non-respiratory, is about 70 sq. m. in ordinary deep respiration. Pütter (1911), basing his work on the data of previous investigators, arrived at some interesting figures. Among his results were 4·5 sq. m. for the secretory surface of the stomach, 48 sq. m. for the absorptive area of the small intestine and 3500 sq. m. for the surface of all the red blood cells.

In line with these investigations, attention has also been directed to the secreting area of the glomeruli of the kidney. Although physiologists are not unanimous regarding the mechanism of the secretion of the urine, there seems to be little doubt that the process begins in the Malpighian corpuscle. The visceral layer of epithelium closely invests the capillary loops of the glomerulus with a thin layer of cytoplasm which acts like a filter, allowing the transudation of water and certain dissolved substances from the blood into the intercapsular space. The present study is concerned with the measurement of the area of this filter. Actually it was not found feasible to measure the epithelium, but since the latter is closely applied to the endothelium of the capillaries, it was decided to ascertain the area of the capillaries.

A review of the literature revealed but two attempts to determine this area. Pütter (1911), using Peter's measurements (1909), multiplied the volume of the renal corpuscle by three in order to obtain the area of the glomerular capillaries; his result was 0·293 sq. mm. Vimtrup (1928) calculated as follows. If it is assumed that the human glomerulus is roughly spherical with a diameter of about 200 μ, its volume is determined by the formula

$$\text{Volume} = \tfrac{4}{3}\pi r^3, \quad r \text{ being } 100.$$

$$\text{Volume} = \tfrac{4}{3}\pi\left(\frac{100}{10^3}\right)^3 = 0{\cdot}0042 \text{ c.mm.}$$

If the entire glomerulus was made up of capillary loops averaging 10 μ in diameter, their total length would be found from the following:

$$\text{Volume of glomerulus} = \tfrac{4}{3}\pi\left(\frac{100}{10^3}\right)^3 \text{ c.mm.}$$

$$\text{Volume of cylindrical tube} = \pi r^2 L \text{ c.mm.} \quad (L = \text{length of tube})$$

$$= \pi\left(\frac{5}{10^3}\right)^2 L.$$

Therefore $$\pi\left(\frac{5}{10^3}\right)^2 L = \tfrac{4}{3}\pi\left(\frac{100}{10^3}\right)^3 \quad (L = 53{\cdot}3 \text{ mm.}).$$

"However, the glomerulus is not made up of capillaries exclusively; a part of it is occupied by the primary and secondary branches of the vasa afferent and efferent, and between the capillary loops as well as between the glomerulus and the Bowman's capsules are narrow free spaces. Probably the capillary loops themselves make up about one-half of the volume of the Malpighian body. We may, then, estimate the total length of the capillary loops in each human glomerulus to be about 25 mm." The surface of the capillaries, which are considered to be cylindrical, will then be 0·78 sq. mm. for each glomerulus.

Vimtrup's result, therefore, is more than twice that of Pütter. Both computations are open to the objection that they involve considerable conjecture. Really the only actual measurement in each case was the diameter of the Malpighian body. Useful as the above figures are, it was felt that a more direct approach to the problem would give more accurate results. The method adopted was to cut serial sections of an injected glomerulus, make outline drawings of the magnified sections, and measure the outline of the capillary walls in each drawing.

MATERIAL AND METHODS

The kidney used was obtained at autopsy from a 6-year-old boy who died of a head injury 7 hours after being struck by a motor car. The kidney was injected 11½ hours after death with carmine gelatin. Small cubes of the tissue were fixed in Allen's fixative PFA_3, a modified Bouin's fluid (McClung, 1929), and serial sections 3 μ thick cut. These were lightly stained with haematoxylin. After careful examination a glomerulus was found which appeared to be completely injected. Using standard projection equipment, outline drawings were then made at a magnification of 1000 diameters. Two typical drawings, Nos. 16 and 43, are shown in the accompanying illustrations. A map measure[1] was used to obtain the total length of the outlines of the capillaries in each drawing. The next step was to cut out wax plates, each 3 mm. thick, using the drawings as patterns; in all, 67 plates were required.

The total length of the outlines in all the drawings was found to be 8431 cm. This does not include the walls of the vasa afferentia et efferentia, which break

[1] This is a simple instrument much used by cartographers to measure the length of irregular lines on maps, such as coast-lines, rivers, etc. It consists essentially of a small toothed wheel mounted on the end of a pencil-like holder and a dial located just above the wheel. As the wheel is moved along the line to be measured the distance traversed is indicated by a needle on the dial.

up into the capillaries shortly after penetrating the glomerulus. It is practically certain that only the capillaries, separated from the intercapsular space by a layer of endothelium and the layer of epithelium forming the visceral portion of Bowman's capsule, take part in the production of the glomerular filtrate. This length, 8431 cm. times 0·3 cm., the thickness of the sections multiplied by 1000, gives a surface area of 2529 sq. cm.

At this stage a correction must be made, in order to allow for the shrinkage which takes place in a tissue from the time it is removed from the body until it is mounted in sections on the slide. This problem, which would seem to be rather an important one, has received less attention than it deserves. In the present work the ideal would have been to select a single injected glomerulus

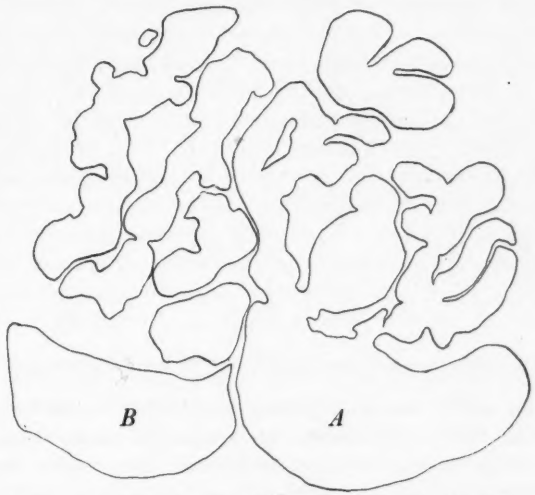


Fig. 1 No. 16 in the series of sections through the injected glomerulus. *A*, afferent arteriole; *B*, efferent arteriole. ×500.

and determine the actual shrinkage of the capillaries. This was not practicable, so several small blocks of rabbit kidney, each in the neighbourhood of 1 c.c., were used as test material. As soon as they were cut out of the kidney they were dried gently on filter paper and the volume determined by the displacement of normal saline in a burette. The tissues were then placed in the same fixative used for the injected glomerulus, Allen's fluid PFA_3, and subsequently subjected to exactly the same dehydration, clearing and impregnation with paraffin. After the proper interval in the second paraffin bath the blocks were taken out, placed in xylol for a minute or two, the excess xylol removed by blotting, and then placed in burette containing xylol. The displacement of the xylol indicated the final volume of the tissue, which was returned to the paraffin bath for a few minutes and then imbedded. By this technique it was

found that the average shrinkage of three blocks of tissue was 42 per cent.[1] Additional shrinkage takes place in the tissue as the liquid paraffin hardens—a process which is easily visualised by observing the cup-like depression seen to develop in a quantity of wax as it cools from 55° C. to room temperature. This increases the shrinkage to 46 per cent. It is quite possible that some of the structures in such a block of tissue would shrink more than others, but it would be a difficult matter to determine this.

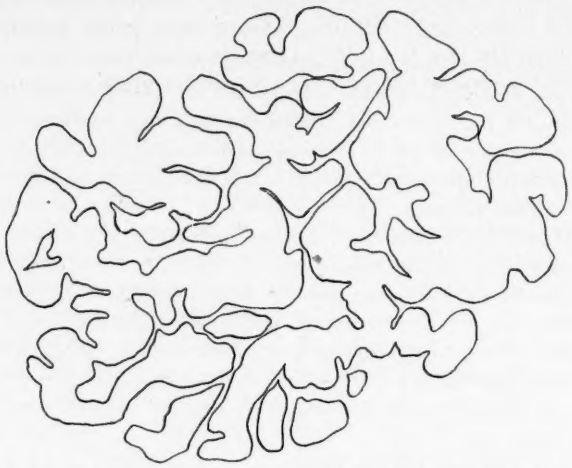


Fig. 2. No. 43 in the series of sections through the injected glomerulus. ×500.

The volume of the magnified glomerulus, as determined by weighing the wax plates, was 1669 c.c. Therefore, the volume before shrinkage would have been 3090 c.c. The surface area of the enlarged glomerulus would then be obtained from the formula

$$A = \left(\sqrt[3]{\frac{x}{y}}\right)^2 B,$$

where A = area of enlarged glomerulus,
B = area of small glomerulus,
x = volume of large glomerulus,
y = volume of small glomerulus,

$$A = \left(\sqrt[3]{\frac{3090}{1669}}\right)^2 2529,$$

$$A = 3813 \text{ sq. cm.}$$

This result, divided by 1,000,000, gives an area of 0·3813 sq. mm. for the capillaries of the actual glomerulus.

[1] When fixation in 10 per cent. formalin in saline was employed, the average shrinkage of two blocks was 33·5 per cent.

In order to arrive at the secreting area of all the glomeruli in one kidney it is, of course, necessary to know the number of glomeruli in a kidney. Again, previous workers have arrived at widely differing answers. Von Möllendorff (1930) has collected the figures from different sources. These vary from 280,000 per kidney (Saeki, 1926) to 4,500,000 (Trout, 1921). Most of the more recent workers, however, have arrived at figures close to 1,000,000 for each human kidney. If we accept this estimate, then the secreting area of all the glomeruli in one kidney would be 0·3813 sq. m., and in both kidneys 0·76 sq. m.

DISCUSSION

It must be remembered that, apart from the technical difficulties, there are several variable factors involved when one attempts to measure the secreting area of the glomeruli. One of these has been alluded to above—the number of glomeruli in the kidney. Naturally, this will depend partly on the size of the organ. Individual differences, too, play a considerable part, for Vimtrup found that in an adult human kidney weighing 143 gm. there were 867,177 glomeruli, while in a kidney weighing 165 gm. there were 1,233,360 glomeruli. In other words, an increase in total weight of the kidney of approximately 15 per cent. was accompanied by an increase in over 42 per cent. in the number of glomeruli. Even more striking is the fact that in the first case the macerated cortex weighed 64·50 gm., while in the second it weighed only 57·10 gm., so that a decrease in the total weight of the macerated cortex was actually accompanied by a large increase in the number of glomeruli.

The age of the individual apparently is of little significance as far as the number of glomeruli is concerned. Certainly no new glomeruli are formed after the first few days of life. Campos (1923) examined the kidneys of forty-three full-term children and found no new glomerulus anlagen. Toldt (1874) and Felix (1905) stated that the new formation of Malpighian bodies continues during the first 8 or 10 days after birth. Moberg's figures (1929) display no constant relation between the age of the subject and number of glomeruli in the kidney.

The most important variable in the secreting area of the glomerular capillaries is the size of the glomerulus itself. This varies greatly even in the same kidney. Most of the determinations in the past were made on fixed tissues, and hence were subject to considerable error. Thus Schweigger-Seidel (1865) found the average diameter of the glomerulus to be 200 μ, Külz (1899) 237 μ, Moore (1904) 210 μ, von Ebner (1902) 130 μ: 220 μ and Prenant (1911) 200–300 μ. Peter's measurements (1909), made from fresh macerated tissues, are probably much more reliable. He measured a number of glomeruli carefully and found that most of them were ovoid in shape, with diameters ranging all the way from 135 to 246 μ. The average diameters of peripheral glomeruli in one subject, a 56-year-old male, were 164 μ: 196 μ.

Many observers have observed that the largest Malpighian bodies are to be found near the cortico-medullary border.

Although the number of glomeruli probably does not increase after birth, their average size shows a marked increase up till adult life. The following table from Eckhardt (1888) shows this clearly:

Number and size of glomeruli per visual field at different ages

Age and sex	Volume of kidney c.c.	No. of glomeruli in a visual field	Diameter μ	
			Glomeruli	Convoluted tubules
Stillborn full-term foetus	6·5	122·1	84·77	—
1-year female	21·0	46·2	87·76	37·63
4-year female	55·0	18·5	149·70	52·72
5-year female	60·0	17·59	148·63	50·50
18-year female	115·0	11·2	189·88	53·65
32-year male	120·0	9·71	213·49	54·76
40-year male	130·0	10·66	193·14	52·72
46-year female	120·0	9·35	195·80	64·76

It is apparent from the above remarks that the number of nephrons in life is fairly constant from birth to adult life, the increase in size of the kidney being due to the increase in size of the glomeruli, increase in length of the tubules and increase in diameter of the tubules.

The Malpighian bodies in Man are not usually spherical, as is often thought, but somewhat ovoid. No doubt oversight of this fact has been responsible for the results of some workers who thought they observed glomeruli of widely differing dimensions when they were simply measuring the greatest diameter in some glomeruli and the smallest in others.

The injected glomerulus used in the present study was located near the medulla and measured $152 \times 178 \times 201\ \mu$ in the mounted sections.

Numerous investigations make it practically certain that in health there is never a time when all the secretory elements in a kidney are functioning at their maximum capacity. The observations of Richards and Schmidt (1924) on the living frog's kidney revealed that the number of glomeruli through which blood flows and hence which function at any one time is only a fraction of the total number of glomeruli in the kidney. This fraction is susceptible of increase and decrease by various agencies. They arrived at the significant conclusion "that the extent of filtration surface in the kidney is variable and a factor which must be of major importance in the adjustment of renal function to secretory requirement".

Finally, the glomerular capillaries, being collapsible tubes, will present a much larger surface for filtration when they are greatly distended with blood than when they contain a minimal quantity of blood. Thus the secreting area of the glomeruli arrived at in this investigation may be taken as the *potential* area, and not as the surface which is constantly in use.

CONCLUSIONS

1. The filtration area of a single typical human glomerulus was found to be 0·3813 sq. mm.

2. Estimations of the total area of all the glomeruli in a single kidney can only be approximate because of the several variables involved. With this reservation in mind, a reasonable figure for the potential surface available for filtration in all the glomeruli of an adult human kidney would be 0·3813 sq. m.

3. In using microscopic sections as a basis for computing the surface area of organs many authors have not paid sufficient attention to the great shrinkage which takes place in tissues subjected to the usual histological technique. Even a modified Bouin's fluid, which is popular with histologists as a fixative, caused shrinkage of nearly 50 per cent. of blocks of kidney.

My thanks are due to a number of individuals for assistance in the course of this work, particularly to Prof. J. R. Cockburn for help with the mathematical computations, and to Miss R. Book, Mr R. M. P. Campbell and Mr V. P. J. Collins for lightening the load of the arduous technical procedures.

REFERENCES

CAMPOS, E. DE S. (1923). (Quoted by Vimtrup.) "Pathological changes in the kidney in congenital syphilis." *Johns Hopk. Hosp. Bull.* vol. XXXIV.

v. EBNER, V. (1902). (Quoted by Von Möllendorff.) Kölliker's *Gewebslehre*, Bd. III.

ECKHARDT, C. T. (1888). "Über die kompensatorische Hypertrophie und das physiologische Wachstum der Niere." *Virchows Arch.* Bd. CXIV, S. 217–45.

FELIX, H. (1905). "Die Entwickelung des Harnapparates." Hertwig's *Handbuch der Vergleichenden Entwickelungsgeschichte*, Bd. III.

KÜLZ, L. (1899). (Quoted by Vimtrup.) "Untersuchungen über das postfoetale Wachstum der menschlichen Niere." Diss. Kiel.

McCLUNG, C. E. (1929). *Handbook of Microscopical Technique*, p. 424. New York: Hoeber.

MOBERG, E. (1929). "Anzahl und Grösse der Glomeruli Renales beim Menschen nebst Methoden diese zahlenmässig festzustellen." *Z. mikr.-anat. Forsch.* Bd. XVIII, S. 271–310.

v. MÖLLENDORFF, W. (1930). "Harn- und Geschlechtsapparat." *Handbuch der Mikroskopischen Anatomie des Menschen*, Bd. VII, Teil 1. Berlin: Springer.

MOORE, F. C. (1904). "The unsymmetrical kidney; its compensatory enlargement." *J. Anat.*, Lond., vol. XXXVIII, pp. 71–81.

PETER, K. (1909). *Untersuchungen über Bau und Entwickelung der Niere*, Bd. I. Jena: Gustav Fischer.

PRENANT, A. (1911). (Quoted by Von Möllendorff.) *Traité d'histologie.*

PÜTTER, A. (1911). "Aktive Oberfläche und Organfunktion." *Z. allg. Physiol.* Bd. XII, S. 125–214.

RICHARDS, A. N. and SCHMIDT, C. F. (1924–25). "A description of the glomerular circulation in the frog's kidney and observations concerning the action of adrenalin and various other substances upon it." *Amer. J. Physiol.* vol. LXXI, pp. 178–208.

SAEKI, T. (1926). (Quoted by Von Möllendorff). "Über die Zahl und Grösse der Glomeruli in der Niere einiger Säugetiere." *Acta Sch. med. Univ. Kioto*, Bd. VIII, S. 189–96.

SCHWEIGGER-SEIDEL, F. (1865). (Quoted by Vimtrup.) *Die Niere des Menschen und der Säugetieren in ihrem feineren Bau.* Halle.

TOLDT, C. (1874). (Quoted by Vimtrup.) "Untersuchungen über das Wachstum der Nieren des Menschen und der Säugetiere." *S.B. Akad. Wiss. Wien*, Bd. XXIX, Abt. 3.

TROUT, A. F. (1921). (Quoted by Von Möllendorff.) "The structural unit of the human kidney." *Contr. Embryol. Carneg. Instn*, vol. LXXV, pp. 103–20.

VIMTRUP, B. J. (1928). "On the number, shape, structure and surface area of the glomeruli in the kidneys of Man and Mammals." *Amer. J. Anat.* vol. XLI, pp. 123–51.

WILLSON, H. G. (1922). "The terminals of the human bronchiole." *Amer. J. Anat.* vol. XXX, pp. 267–95.

THE INNERVATION OF THE PERIODONTAL MEMBRANE

By W. LEWINSKY and D. STEWART

Department of Anatomy, The University, Manchester

Until recently very little was known about the innervation of the periodontal membrane, and the only information of any value is to be found in a paper by Dependorf published in 1913 (2). This investigation states that the nerve bundles form coarse and fine networks and end in fine, pointed processes, particularly in the cementoblast region. During the last few years, however, several important papers have been published which have considerably increased our knowledge of this subject.

The earliest of these investigations was performed by Kadanoff (3). From his earlier researches into the innervation of similar tissues, such as tendon, ligaments, periosteum and dura mater, it appeared to him that Dependorf's conclusions were faulty and that that author had not obtained complete impregnation of the nerve endings. Dependorf had used extracted teeth and Kadanoff considers that the periodontal membrane had probably been damaged. He himself obtained his material from two individuals who had suffered death by judicial hanging. He secured the tooth and its alveolus in one piece, and after decalcification stained them by Bielschowsky's method to demonstrate the nerve fibres. According to this worker, the fibres from the apical region run vertically towards the gingival margin and at intervals are reinforced by bundles entering the periodontal membrane through the foramina in the alveolar process. The nerve fibres given off from the main bundles end in what appeared to be terminal plexuses, but that there was no actual anastomosing of the terminal fibres. Some of the terminal fibres ended in small knob-like swellings, but no encapsulated nerve endings were found. He disagrees with Dependorf's view that most of the nerves end in the cementoblast layers, and states that the fibres which do enter form loops therein and return to end in the connective tissue of the membrane.

Van der Sprenkel has recently published three papers on this subject (4,5,6). He used horizontal sections of the mandibles of young mice stained by the de Castro-somniform method. According to him, the majority of the nerve fibres probably enter the membrane through the alveolar processes. In the membrane they end in three ways:

(1) Reticulated rings close to the bony alveolus.

(2) Terminal reticula around the nuclei of the peripheral layers of the membrane.

(3) Networks in the more centrally placed part of the membrane from which fibres arise which pass through the cementoblasts and enter the tubules of the dentine.

Bradlaw has during the last month published a paper on the innervation of the teeth (1). He very kindly lent a copy to us and also prints of his excellent photomicrographs, and we should like to take this opportunity of thanking him for allowing us to read his paper prior to its publication.

Bradlaw has been unable to find the terminal rings of van der Sprenkel but has seen the neural loops of Kadanoff turning back from the cementum. He has also seen structures which appear to be terminal coils near the cementum, and these are very clearly demonstrated in his photomicrographs.

METHOD

Our material is open to the same criticism which Kadanoff brought against Dependorf's specimens. However, in this country such valuable sources of material as those available to Kadanoff are not open to the investigator. Therefore, as we desired to study the human teeth, we have had to be contented with extracted teeth which had portions of the alveolus attached. It is realized that in these specimens there is a possibility that during extraction damage may have been done to such fine structures as the nerve fibres. On the other hand, we have seen little sign of this and have been able to trace fine nerve fibres for considerable distances without discovering any signs of rupture. It certainly has caused no gross damage in the extensive region of the membrane which remains firmly attached to both the alveolus and the cementum of the tooth (Pl. I, fig. 4).

The teeth were prepared for examination by fixation in ammonia alcohol, decalcification in 5 per cent. nitric acid and impregnation by the ordinary Cajal technique. They were then embedded in paraffin and cut in serial longitudinal sections at 12 μ thickness. Many dental histologists have declared that it is impossible to cut serial sections of teeth which have been embedded in paraffin, but this has not been the experience of the members of this department. Serial sections have been employed by Manley in his investigations into the reactions of the pulps to filling material, and the technical staff have little difficulty in cutting through a whole tooth in this way. By this method it was possible to trace the course of the nerve fibres of the periodontal membrane for long distances by following them from section to section. It would probably have been more satisfactory if the thickness of the sections could have been increased, but unfortunately when this was done they curled up and could not properly be flattened on the slide.

To record the course of the fibres, sketches (Text-figs. 1, 2 and 3) were constructed with the camera lucida. A drawing of a section was made which included the edge of the tooth and the alveolus, and all the nerve fibres or portions of nerve fibres in that part of the periodontal membrane visible in

the field were then sketched in their correct position. The equivalent field of the next section was then placed under the microscope, and the slide was

Text-fig. 1.

Text-fig. 2. * This nerve ending is the same as that shown by a similar mark in Plate I, fig. 3.

adjusted to allow images of the principal landmarks to fall on the corresponding positions of the drawing of the previous section and any additional fibres were sketched in. This process was continued, if desired, with a third

section, and in this way a linear reconstruction was made of the course of the nerve fibres through two or more sections.

Text-figs. 1 and 2 are three sections and Text-fig. 3 two sections reconstructed. Photomicrographs (Pl. I, figs. 1 and 2) were made from the same field at different depths of focus, of one of the sections used in constructing Text-fig. 1. Photomicrographs (Pl. I, figs. 3 and 4) correspond to Text-figs. 2 and 3 respectively. If the photomicrographs are compared with the sketches, it will be seen that these give a very accurate idea of the course of the fibres.

Text-fig. 3.

RESULTS

The nerve fibres of the periodontal membrane come from the apical region of the tooth and run towards the gum in longitudinal bundles in company with the blood vessels. These bundles communicate with each other and are reinforced in their course by fasciculi which enter the membrane through foramina in the alveolar process.

As they proceed towards the gingival margin, individual fibres leave the main bundles at intervals and after a short course divide dichotomously into small branches. If these are traced to their terminations, they are found to break up into fine arborizations as seen in Text-figs. 1, 2 and 3. These arborizations resemble the terminal networks in appearance, but, like Kadanoff, we have been unable to detect any fusion of the terminal fibres with each other. Many of these fibres end in small rounded bodies. These end-organs are seen in the linear reconstructions and are clearly demonstrated in photomicro-

graphs (Pl. I, figs. 2 and 3). In the latter the continuity of the end-organ and fibril with the main branch is lost, but if Text-fig. 2 be examined, it will be seen that it has been possible to bridge the gap, as the missing portion of the fibril was present in the adjoining section. Some of these endings appear to be in direct contact with the cells of the periodontal membrane, but it is doubtful whether this is of any great significance as many of them seem to have no relationship to these structures. These rounded endings resemble the structures seen by Kadanoff, but unfortunately his paper contains no photomicrographs, so that it is impossible to compare the two structures with certainty.

We have been unable to trace nerve fibres into the cementum of the tooth; we have, however, observed the recurrent loops described by Kadanoff and Bradlaw, made by nerve fibres turning back on their course after approaching the cement. Bradlaw's terminal coils, which are similar but more complex structures, were not found, but he has given such a clear demonstration of them in his photomicrographs that there can be no doubt that they are present in the membrane. The cause of this discrepancy in our results may be due to the fact that Bradlaw obtained his material from the monkey, and it is possible that these structures are not present in the human tooth.

Like Bradlaw, we have been unable to discover the end rings of van der Sprenkel, and, as already mentioned, like Kadanoff and Bradlaw, we have been unable to trace any nerve fibres through the cementum into the dentine. It is greatly to be regretted that van der Sprenkel only illustrates his paper with drawings, as a few photomicrographs would have been of great assistance to other workers in this field, his findings are completely at variance with those of other writers on this problem. However, these discrepancies may be due to the material which van der Sprenkel used, and the innervation of the periodontal membrane of the mouse may be markedly different from that of the primates.

SUMMARY

The nerve fibres of the periodontal membrane end in fine arborizations, many of which have a terminal knob-like body. None of the fibres could be traced into the cementum of the tooth, and the rings of van der Sprenkel were not seen.

ACKNOWLEDGEMENTS

We desire to thank Prof. Stopford for facilities in carrying out this work and Prof. Wilkinson for material. The photomicrographs we owe to the skill and care of Mr Gooding.

REFERENCES

(1) Bradlaw, R. (1936). *Proc. roy. Soc. Med.* vol. xxix, pp. 507–18.
(2) Dependorf (1913). *Dtsch. Mschr. Zahnheilk.* Bd. xxxi, S. 853–64.
(3) Kadanoff, D. (1929). *Verh. phys.-med. Ges. Würzburg*, N.F., Bd. liv, S. 27–32.
(4) van der Sprenkel, H. B. (1935). *Revue odontol.*
(5) —— (1935). *Z. mikr.-anat. Forsch.* Bd. xxxviii, S. 1–86.
(6) —— (1936). *J. Anat.*, Lond., vol. lxx, pp. 233–41.

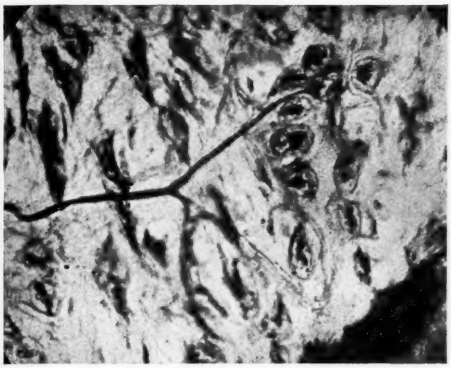


Fig. 1.

Fig. 2.

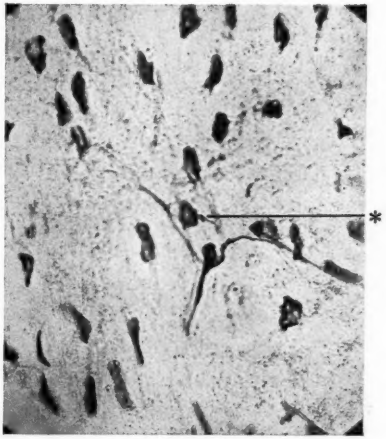


Fig. 3.

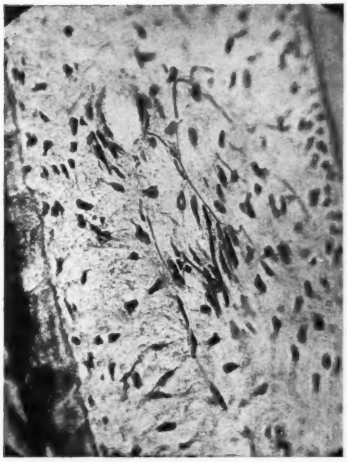


Fig. 4.

* This nerve ending is the same as that shown by a similar mark in Text-fig. 2.

UNIV. OF MICH.

THE UTERINE VEIN ENTRIES IN THE RABBIT

By K. J. FRANKLIN, D.M., M.R.C.P.
and A. D. McLACHLIN, M.D., M.Sc.

University Department of Pharmacology, Oxford

In the course of studies upon the stream lines of blood in the abdominal vena cava of the rabbit (2, 3) we observed that the uterine veins entered the iliac veins by peculiar bulbous endings, which were usually dimpled in the middle. The swollen terminations of the uterine veins were frequently wider than the iliac veins into which they emptied. All these features are shown in Fig. 1.

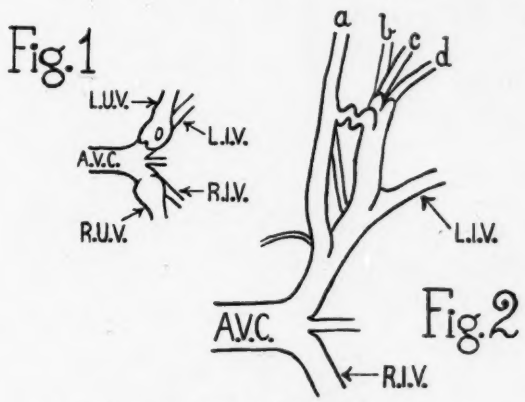


Fig. 1. Usual appearance of uterine vein entries.

Fig. 2. Illustrating uterine vein entries in exceptional case.

A.V.C. abdominal vena cava; *L.I.V.* left iliac vein; *R.I.V.* right iliac vein; *L.U.V.* left uterine vein; *R.U.V.* right uterine vein; *a, b, c,* veins draining part of uterine arcade; *d,* vesical vein.

The corresponding veins in the male have similarly shaped terminations, though these are naturally on a smaller scale than those of the *pregnant* female.

The uterine veins carry most of the uterine and part of the vesical blood. The corresponding veins in the male similarly carry part of the vesical blood; they also drain the vasa deferentia and probably the uterus masculinus, into which the vasa deferentia open. Langley & Anderson (4) stated that the uterus

masculinus of the rabbit was two-horned, was commonly called "the seminal vesicles", and occasionally "the prostatic vesicle". At all events, the veins we are describing seem to drain the adult structures developed from the Müllerian-Wolffian system, and are to that extent analogous in the two sexes.

It occurred to us that the bulbous dimpled endings might be caused by partial fusion of veins and, after looking at a number of animals, we eventually found one which supported this hypothesis. On dissection we discovered the venous pattern shown in Fig. 2. Two main veins entered the left iliac vein. The left-hand one in the figure came from the uterine arcade. The right-hand one in the figure was formed by the union of three smaller veins, two carrying blood from the uterine arcade and the third from the bladder. These two main veins were close together until separated by dissection; they were united by an anastomosing vein, as shown, a short distance distal to their entries into the iliac vein. A small vein also passed from the left-hand vein, just at the level of the anastomosing vein, to enter separately into the iliac vein. There can be little doubt that the constituents of the uterine vein normally fuse more completely except just at their terminations. Presumably incomplete fusion here produces the bulbous ending and its accompanying dimple.

SUMMARY

The bulbous ending of the uterine vein in the doe rabbit, and of the corresponding vein in the buck rabbit, is described and a suggestion made as to its causation.

REFERENCES

(1) Borradaile, L. A. (1935). *Manual of Zoology*, p. 507.
(2) Franklin, K. J. & McLachlin, A. D. (1936). *J. Physiol.* vol. lxxxvi, p. 386.
(3) —— —— (1936). *J. Physiol.* vol. lxxxvii, p. 87.
(4) Langley, J. N. & Anderson, H. K. (1895–6). *J. Physiol.* vol. xix, p. 124.

THE EXTERNAL CONFIGURATION OF THE CEREBRAL HEMISPHERES OF THE CHIMPANZEE[1]

By A. EARL WALKER, M.D.[2] and JOHN F. FULTON, M.D.

From the Laboratory of Physiology, Yale University School of Medicine

It is essential to know the normal surface markings of the cerebral cortex of experimental animals which are to be employed for study of cortical functions. During the past six years the chimpanzee has been extensively used for study of the frontal lobes (Fulton, 1936). A study by one of us (A. E. W.) of the thalamic projections to the cortex of this anthropoid is also now in progress. It has seemed desirable therefore to describe in some detail the convolutional markings of the chimpanzee, but no attempt will here be made to correlate these external markings with cytoarchitecture.

Individual brains have been observed by several anatomists (Pansch, 1868; Bischoff, 1870; Wernicke, 1876; Chapman, 1879; Hervé, 1888; Müller, 1888; Giacomini, 1889; Beddard, 1895; Benham, 1895; Dwight, 1895; Parker, 1896; Retzius, 1906; Fischer, 1921), but no large series was reported until Mingazzini (1928) in an excellent survey described the topography of some fifteen chimpanzee brains. Several writers have studied the chimpanzee brain in a comparative series (Vrolik, 1841; Pansch, 1868; Hamy, 1872; Bischoff, 1877; Broca, 1888; Cunningham, 1886; Flatau & Jacobsohn, 1899; Zuckerkandl, 1908). Waldeyer (1895) gives a good review of the literature up to 1895. More recently Tilney & Riley (1928) and Ariens Kappers (1929) have made studies on the comparative anatomy of the cortical markings of the primates.

The present survey is based upon a study of seventeen chimpanzee brains, from which twenty-nine hemispheres were available for examination. The majority of the brains had been injected with formalin at autopsy and preserved in 10 per cent formalin. A few were hardened in alcohol. In order to facilitate the examination of the convolutional markings the pia was stripped from the cortex. In some of the brains cortical ablations had been made, thus rendering a portion unsuitable for study, but in many the entire cortex was intact. The majority of the chimpanzees (fifteen) were aged between 3 and 8 years; one was a 2 months old baby, and the other a mature female aged 12. The configuration of the brains of the two animals at the extremes of age did not show abnormal variations. The external configuration of the brain of the baby chimpanzee was but a miniature of that of an adult cerebral hemisphere. The terminology adopted for this paper is that employed by Mingazzini (1928).

[1] This work was aided by grants from the Research Fund of the Yale University School of Medicine and the Rockefeller Foundation.

[2] Fellow of the Rockefeller Foundation.

I. PRIMARY FISSURES

The Sylvian fissure and insula. The Sylvian fissure, as in the human cortex, begins on the basal surface of the brain and extends laterally between the temporal and frontal lobes (Pls. I and II). In the human brain the horizontal, ascending and posterior rami may be recognized, but in the chimpanzee brain only the posterior ramus is present. Certain authors, notably Broca (1888) and Hervé (1888), have described an anterior limb, but, as Cunningham points out, the fissure which they observed does not correspond in position with the ascending limb of the Sylvian fissure in man. It cuts the operculum behind the precentral sulcus, while in man the ascending limb always lies well anterior to this sulcus. Moreover, the ascending ramus divides the frontal and orbital opercula in the human brain, while in the chimpanzee these are absent, only the temporal and fronto-parietal opercula being recognizable. In less than 20 per cent of the cases in the present series a small branch called the sulcus opercularis ascended a varying distance into the inferior part of the precentral convolution (Pl. IV, Fig. 1). A small fissure quite similarly placed, but not anastomosing with the Sylvian fissure, is occasionally present, usually when the sulcus opercularis is absent. It is the sulcus subcentralis anterior (Pl. II, Fig. 1).

The posterior branch of the Sylvian fissure extends on the lateral surface of the hemisphere for 4–5 cm., generally ending singly but occasionally bifurcating. Not infrequently a small ramus (the sulcus subcentralis posterior) is given off just behind the central sulcus. This extends superiorly for 1–1·5 cm. Usually no other branches are given off. The fissure is quite deep in its entire extent, measuring 1·5–2 cm. to the bottom.

The insula (Island of Reil, *IR*, Pl. IV, fig. 2 and Pl. V, fig. 1) is that portion of the cortex which is covered by the two opercula—parieto-frontal and temporal. As Cunningham (1886) suggests, it is likely that a portion of the insula, as it exists in man, is equivalent to the inferior part of the precentral convolution of the chimpanzee brain, which, owing to the absence of the frontal opercula, is exposed to view. The sulci and convolutions of the island of Reil are poorly developed (Pl. IV, fig. 2 and Pl. V, fig. 1). The limiting furrow is frequently indistinct anteriorly, although inferiorly it is quite deep. On the surface of the insula usually two more or less distinct sulci can be recognized. The more anterior and superior runs in the plane of the central sulcus, and is hence comparable to the sulcus centralis insulae, the second is on an oblique plane parallel to that of the Sylvian fissure. Hence there are three convolutions on the surface of the insula, a single short gyrus and two long ones. In some brains these are well defined, but in the majority the sulci are poorly developed, and the convolutions but slight ridges.

The central sulcus. This is a constant sulcus dividing the frontal from the parietal lobe (Pls. I and II). Though very deep in the chimpanzee it generally does not reach to the sagittal sulcus. Mingazzini (1928) states that it extends to

the medial surface of the hemisphere in only 10 per cent of cases. Its contour is quite irregular, but in most brains two anterior angulations are present, one in the upper portion and a second near its lower end. These angles cause the middle part of the sulcus to have an anterior concavity. The fissure is quite deep, extending beneath the surface of the hemisphere for 1·5–1·8 cm. Toward the lower portion it is more superficial, reaching inward only 1 cm. The lower portion of the sulcus is not interrupted as in the human brain, and usually ends without bifurcating. No branches are given off as a rule, but occasionally near its anterior extremity a rudimentary fissure may extend forward for 5–8 mm.

The parieto-occipital fissure. This is a deep fissure which divides the parietal and occipital lobes both on the lateral and medial surfaces (Pls. I and II). On the lateral surface the sulcus is known as the sulcus parieto-occipitalis externa and on the medial surface as the parieto-occipitalis interna. The medial or internal branch descends to end just posterior to the corpus callosum on the inferior surface of the occipital lobe separated from the calcarine fissure by the gyrus cunei. The external branch extends laterally for 5·5 cm. and not infrequently gives off several branches. In 60 per cent of cases the intraparietal sulcus anastomoses with the external parieto-occipital fissure about 2 cm. from the midline. Beddard (1895) noted that the posterior wall of the external parieto-occipital sulcus is markedly convoluted. These ridges may bridge across the external parieto-occipital fissure, usually obliquely. Three ridges are frequently present, the most superior of which is quite superficial, and the other two deeply embedded in the sulcus. Gratiolet (1850) described these as "plis de passage". Many authors have since commented on them (Turner, 1866; Holl, 1907, 1908 *a*, *b*, *c*; Smith, 1904). When the bridging convolutions are well marked and superficial, the internal and external parieto-occipital fissures may not anastomose at the midline (Pl. III, fig. 1 and Pl. V, fig. 2). Tilney & Riley (1928) infer that this is the usual condition in the chimpanzee brain, but in the present series such superficial bridging convolutions were found in less than a third of the brains.

II. THE FRONTAL LOBE

The frontal lobe consists of the portion of the hemisphere anterior to the central fissure and above the Sylvian fissure. It is divided into three surfaces, a lateral, medial and inferior or orbital.

A. *Orbital* (Pl. IV, fig. 1). On the orbital surface of the brain are several constant sulci, the olfactorius, orbitalis, opercularis and orbito-frontalis. The sulcus olfactorius (Pl. IV, fig. 1, *O*) extends anteriorly along the midline of the orbital surface of the frontal lobe concealed by the olfactory tract. It is always linear and does not branch. The orbital sulci (Pl. IV, fig. 1, *OS*) just lateral to the olfactorius frequently have a Y-shape, or occasionally an irregular H-shape. They may be completely divided into two separate and roughly parallel linear sulci. On the lateral aspect of the frontal lobe are two inconstant fissures, the sulcus orbito-frontalis which runs from the posterior part of the

orbital surface laterally along the lateral margin of the frontal lobe, and the sulcus opercularis which is a short sulcus quite inconstant and frequently described as a branch of the Sylvian.

B. *Lateral surface* (Pls. I and II). The lateral surface of the frontal lobe may be divided into the precentral and the frontal convolutions.

The precentral convolution. This gyrus is a large smooth convolution in front of the central sulcus bounded anteriorly by the precentral sulci. Occasionally it is divided by a sulcus cutting across its lower third. It is always larger than the postcentral convolution and always wider at its superior extremity than in the opercular region. It may be much better developed on one side than on the other.

Precentral sulci. The precentral sulci (Pl. I, fig. 2 and Pl. II, fig. 1, *PS*) consist of two fissures, a superior and an inferior. The superior, usually short, parallels the upper part of the central sulcus and anastomoses in many cases with the posterior end of the superior frontal sulcus. It is undoubtedly homologous with the superior precentral sulcus of the macaque monkey. The inferior precentral sulcus (Pl. II, fig. 2, right, *PRI*) is very variable, being usually longer than the superior and running in a more horizontal plane. Usually it gives off from its middle the inferior frontal sulcus.

Frontal sulci (Pl. II, figs. 1, 2 and Pl. III, fig. 1). In general the more rostral sulci of the frontal lobe are roughly parallel and run anteriorly as in the human brain, and they may be readily homologized with the latter. As just mentioned, the superior frontal sulcus (Pl. II, fig. 2, right, *IF*) frequently takes origin from the superior precentral. Rarely does it extend to the frontal pole unbroken, usually bifurcating and ending 2–3 cm. in front of its origin, from in front of which an irregular sulcus extends towards the frontal pole. Not infrequently the sulcus is broken by transverse fissures. Its contours being quite irregular. The inferior frontal sulcus (Pl. II, figs. 1, 2 and Pl. I, fig. 2, *IF*) is often derived from the middle part of the inferior precentral sulcus and extends rostrally for a variable distance. It usually does not anastomose with the fronto-marginal sulcus, but runs above it almost to the tip of the frontal pole. The fronto-marginal sulcus is quite variable. It extends along the inferior border of the lateral surface to the frontal pole. Occasionally it is divided into two segments—a medial and a lateral.

The frontal gyri. As in the human brain the gyri of the frontal lobe may be divided into the superior, middle and inferior by the superior and inferior frontal sulci respectively (Pl. II). The superior frontal gyrus lies above the superior frontal sulcus, and not infrequently is derived by two roots—one from the superior part of the precentral gyrus and the second from below the superior precentral fissure. The convolution occasionally has irregular tertiary sulci. The middle frontal gyrus is bounded by the superior and inferior frontal sulci and generally is derived from one root from the precentral convolution near its upper third. It has occasional irregular tertiary sulci. The inferior frontal gyrus is divided into two parts, a posterior, pars opercularis, and an

anterior, pars triangularis. The former is bounded by the sulcus opercularis posteriorly and the inferior precentral sulcus superiorly and anteriorly. It has a root from the inferior end of the precentral sulcus, and passes over anteriorly into the pars triangularis. This is a curved convolution surrounding the end of the fronto-orbital sulcus. These divisions are not constant and the opercular part may be entirely absent.

III. THE PARIETAL LOBES

The parietal lobe is bounded by the central fissure anteriorly, the parieto-occipital fissure posteriorly and the Sylvian fissure and its arbitrary posterior extension inferiorly. The lobe is divided by the postcentral and intraparietal sulci (Pls. I and II).

Postcentral sulcus. This is a deep fissure running parallel to the central sulcus from a point 6–8 mm. lateral to the interhemispheral fissure. It ends by bifurcating just above the Sylvian fissure, the anterior passing forward, and the posterior inferiorly.

In more than half the cases this is a single undivided fissure, but in the remainder the sulcus is split near the inferior third. When the sulcus is undivided the intraparietal fissure generally joins it near its middle; if divided, the intraparietal fissure joins with its inferior portion, only very rarely with the superior part.

Intraparietal sulcus. This fissure divides the parietal lobe into two parts, a superior and inferior parietal lobule. As mentioned above, it anastomoses with the middle of the postcentral fissure when the latter is single, and with the inferior postcentral sulcus when it is divided. It runs posteriorly, more or less parallel to the midline, to bifurcate near the parieto-occipital fissure, the upper branch ending singly near the latter fissure and the lower descending frequently to anastomose with the first temporal sulcus.

Postcentral convolution. This convolution is frequently poorly developed, and always much smaller than the precentral. In the inferior part the sulcus subcentralis posterior may divide off a gyrus subcentralis posterior.

Superior parietal lobule. This quadrilateral cortex bordered by the postcentral sulcus, the parieto-occipital and the intraparietal sulci varies greatly in shape and size even on the two sides. There may be one irregular, generally sagittal fissure in this lobule, the superior parietal sulcus of Retzius. It may join the postcentral fissure or the marginal branch of the calloso-marginal sulcus. The latter passes from the medial on to the lateral surface of the hemisphere just posterior to the postcentral fissure. Rarely there are other tertiary sulci in this lobule.

Inferior parietal lobule. The inferior parietal lobule is composed of two parts, the supramarginal gyrus which surrounds the Sylvian fissure and the angular gyrus about the termination of the first temporal fissure.

Supramarginal gyrus (Pl. II, fig. 2, *SM*). This gyrus has many variations. It usually receives an anterior root from the lower part of the postcentral

convolution and ascends about the posterior extremity of the Sylvian fissure to the posterior part of the first temporal convolution. Its shape and size vary greatly not only in different animals but in the two hemispheres of the same animal. It rarely has tertiary fissures.

Angular gyrus (Pl. II, fig. 2, *A*). This cortex swings around the anterior end of the first temporal fissure. It lies between the intraparietal and parieto-occipital fissures. Its shape and size are quite variable.

IV. THE TEMPORAL LOBE

The temporal lobe lies inferior to the Sylvian fissure and anterior to the arbitrary continuation of the parieto-occipital fissure on the lateral surface of the hemisphere. It contains four sulci and five convolutions (Pls. I and II).

Temporal sulci. The superior temporal sulcus runs from the temporal pole parallel to the Sylvian fissure at the posterior extremity of which it turns vertically upward to end in the supramarginal gyrus in two branches. These end in the angle between the intraparietal and parieto-occipital fissures. It may anastomose with the intraparietal, parieto-occipital, or the Sylvian fissure. The middle temporal sulcus rarely runs an unbroken course from the temporal pole to the parieto-occipital fissure. It usually consists of two or three separate and irregular small fissures, thus only incompletely dividing the middle and inferior temporal gyri. The second or middle temporal sulcus is frequently related to the sulcus occipitalis inferior, a small vertical temporal gyrus. The second or middle temporal sulcus is frequently related to the sulcus occipitalis inferior, a small vertical fissure just anterior to the lower part of the parieto-occipital sulcus. When the middle temporal sulcus extends to the parieto-occipital fissure the inferior occipital is generally absent, but when the first is rudimentary the latter is well developed. The basal occipito-temporal sulci consist of the collateral sulcus and the more lateral inferior temporal or sulcus occipito-temporalis lateralis. Although earlier writers did not differentiate these sulci, Mingazzini (1928) believes that they should be distinguished. The inferior temporal is quite short and the collateral is long (Pl. III, fig. 1).

Temporal gyri. The superior temporal gyrus is a well-defined convolution lying between the Sylvian fissure and the superior temporal sulcus. On its upper surface posterior to the inferior end of the central sulcus are frequently seen one or two transverse elevations which represent the transverse temporal gyri. These may be traced to the depth of the limiting fissure of the insula (Pl. IV, fig. 2 and Pl. V, fig. 1). In two-thirds of Mingazzini's (1928) cases there were two gyri, the posterior one being the most frequently absent. Holl (1908*b*) has noted similarly placed elevations in lower primates even in the macaque brain—a fact which is of great significance. The middle temporal gyrus is usually well differentiated although its lower margin may not be well defined owing to the division of the middle temporal sulci into several distinct fissures. The posterior part of the middle temporal gyrus is frequently divided into two roots the one going to the angular gyrus and the lower to the proximal part of

the occipital lobe. The inferior temporal gyrus is poorly defined and quite variable. The occipito-temporal gyri are not well defined. The lobulus fusiformis lies between the inferior temporal and the collateral fissures, and the lobulus lingualis between the collateral and hippocampal fissures. The divisions between these are however frequently indefinite.

The rhinal fissure is readily recognized at the medial angle of the temporal lobe where it borders the hippocampal gyrus. It runs anteriorly into the Sylvian fissure.

V. THE OCCIPITAL LOBE

The occipital lobe is bounded anteriorly by the parieto-occipital fissure. It presents three surfaces, a lateral, medial and inferior. The lateral surface is relatively small as compared to the lateral surfaces of the other lobes of the cerebrum.

Sulcus occipitalis diagonalis. The lateral surface presents only one constant sulcus, the sulcus occipitalis diagonalis, which may begin at the occipital pole but frequently starts considerably in front of this point and runs obliquely forward. Its shape is quite variable; usually it is somewhat curved with its concavity medial, but it may be straight. In a considerable number of cases a branch runs mesially from its middle. Tertiary sulci are common.

Precuneus. This is bounded anteriorly by the incisura cinguli and posteriorly by the sulcus parieto-occipitalis interna. Its size is quite variable. The sulcus subparietalis is a quite constant fissure which runs ventrally from the posterior part of the cingular gyrus. Occasionally a sulcus runs vertically upward almost parallel to the internal parieto-occipital. This is known as the sulcus precunei.

Cuneus. As in the human brain this is bounded by the internal parieto-occipital and calcarine fissures. Owing to an internal bridging convolution, the gyrus cunei, these sulci rarely anastomose as they do in the human brain. This fact has been mentioned by many authors (Mingazzini, 1928; Chapman, 1879; Cunningham, 1886).

The calcarine fissure. This is a constant fissure on the inferior surface of the occipital lobe extending from a point about 1 cm. lateral to the midline beneath the splenium of the corpus callosum to the occipital pole. It reaches the lateral surface of the hemisphere and ends by bifurcating, one limb passing anteriorly and the other posteriorly. Occasionally it ends singly. Infrequently small branches are given off but usually it is linear. This fissure is quite deep, reaching inward for 1·5–2 cm.

VI. THE MEDIAL SURFACE OF THE BRAIN (EXCLUSIVE OF OCCIPITAL LOBE)

Sulcus calloso-marginalis. The medial surface of the brain presents several sulci but the most constant is the sulcus calloso-marginalis (Pl. III, figs. 1 and 2). This takes its origin just anterior to the genu of the corpus callosum, and

ascending to its superior surface runs parallel to it, occasionally sending small branches to the neighbouring gyri. It ends posteriorly generally by bifurcating, one branch (incisura cinguli) ascending to the lateral surface of the hemisphere at the level of the splenium of the corpus callosum and the second branch (sulcus subparietalis) continuing posteriorly for a varying distance. Mingazzini (1928) considers that the size of the precuneus depends to some extent at least on the length of this posterior branch. Occasionally the calloso-marginal fissure is broken into two distinct sulci, the anterior one usually being the smaller.

On the medial surface of the brain anterior to the rostrum of the corpus callosum are several small more or less horizontal sulci, the sulci rostrales. Frequently there are two, being designated as dorsal and ventral. The callosal sulcus as in the human lies immediately above the corpus callosum, and rarely has branches passing to the gyrus cinguli.

Medial gyri. The gyrus fronto-parietalis medialis lies above the calloso-marginal sulcus. It is often divided by transverse sulci running from the calloso-marginal fissure. Frequently there is a sulcus passing upward—the para-rolandic—which marks the posterior limit of the paracentral lobule. The gyrus cinguli lies between the sulcus callosus and calloso-marginalis. Owing to the variations in the posterior limb the posterior portion of the calloso-marginal sulcus is quite variable.

DISCUSSION

From the foregoing description it is evident that the convolutional markings of the chimpanzee brain are quite variable. These variations are not only seen in different brains but the two hemispheres of the same brain differ greatly (Pl. II, fig. 2). While these variations are most pronounced in the secondary sulci, even the primary fissures are not constant. In most mammals and in the monkeys (excluding baboons) the cortical markings tend to be quite constant in the same species.

Certain homologies in the brain of monkeys, anthropoids and man are readily apparent. The central sulcus is a constant feature of monkey, baboon, chimpanzee, orang, gorilla and man. Likewise the Sylvian fissure is readily recognized in these animals. In the monkeys the Sylvian fissure anastomoses with the first temporal, so that the supramarginal and angular gyri are poorly developed in these species. The parieto-occipital fissure is readily recognized in the anthropoids and man and in the lower primates it is represented by the simian sulcus (Smith, 1904). The bridging convolutions are much better developed and more superficial in the orang brain and in the human brain than in the chimpanzee, so that the internal and external parieto-occipital fissures are interrupted at the midline. In the one gorilla brain at our disposal the first bridging convolution was submerged, thus conforming to the type seen in the chimpanzee.

The fissures of the frontal lobe of the chimpanzee find ready homologies in man, but less well-defined analogous structures are present in the monkeys. The superior precentral sulcus is but a small indentation in the superior portion of the precentral convolution in the macaque monkey. Even in the baboon, although better developed, it is still small; in the gibbon it is much larger. The inferior precentral sulcus in the lower primates is well developed. The frontal sulci and gyri are similar in the anthropoids and man, varying mainly in the complexity of the convolutions as the result of tertiary fissures. In the lower primates the superior frontal sulcus, like the superior precentral, is quite small, but becomes progressively larger as the phylogenetic scale is ascended.

The markings of the parietal lobe of the chimpanzee, orang and gorilla are quite comparable; in man this region is more complex. In the anthropoids the development of the supramarginal and angular gyri is out of all proportion to that of the superior parietal convolutions. In the monkeys the configuration of the parietal lobe is very simple, and it is difficult to be certain of the homologies. The intraparietal fissure of the macaque monkey probably represents both the inferior postcentral and the intraparietal sulci.

The markings of the temporal lobe are much more uniform in the various species than those of the parietal lobe, and the homologies present little difficulty. The occipital lobe, in particular the lateral surface, differs markedly in the anthropoids from that in the monkeys. Owing to the enormous development of the angular and supramarginal gyri, the striate cortex is pushed on to the medial surface of the hemisphere. In man the calcarine fissure and striate cortex reach to the lateral surface of the occipital lobe; in anthropoid brains small amount of striate cortex is present on the lateral surface. For this reason it is evident that the greater part of the lateral surface of the occipital lobe in the anthropoid and man has no homology in the lower primates (Smith, 1904). In the anthropoids the calcarine and parieto-occipital sulci do not usually anastomose, an internal bridging convolution, the gyrus cuneus, intervening. In man this gyrus is submerged in the calcarine sulcus, and the two fissures join. Except for this difference the relations of the cuneus and precuneus in the anthropoids and man are comparable.

The markings on the medial surface of the hemisphere are readily homologized in the anthropoids and man and require no special comment.

SUMMARY

1. A detailed description of the external configuration of the cerebral hemispheres of the chimpanzee is presented.

2. The homologies of these in man, anthropoids and monkeys are discussed.

ABBREVIATIONS

The following abbreviations have been used in the illustrations:

A	Gyrus angularis.	*PC*	Gyrus precentralis.
C	Sulcus centralis.	*PCC*	Gyrus postcentralis.
CF	Sulcus calcarinae.	*PCI*	Gyrus postcentralis inferior.
CI	Sulcus cinguli.	*PCS*	Sulcus postcentralis superior.
CO	Sulcus collateralis.	*PE*	Sulcus parieto-occipitalis externus.
FM	Sulcus fronto-marginalis.	*PI*	Sulcus parieto-occipitalis internus.
FPM	Gyrus fronto-parietalis medialis.	*PR*	Lobulus precunei.
F 1	Gyrus frontalis superior.	*PRI*	Sulcus precentralis inferior.
F 2	Gyrus frontalis medianus.	*PS*	Sulcus precentralis superior.
F 3	Gyrus frontalis inferior.	*R*	Sulcus rhinalis.
GC	Gyrus cinguli.	*S*	Sulcus Sylvii.
H	Gyrus hippocampi.	*SA*	Sulcus subcentralis anterior.
I	Sulcus intraparietalis.	*SC*	Sulcus calloso-marginalis.
IF	Sulcus frontalis inferior.	*SCU*	Sulcus cunei.
IT	Sulcus occipito-temporalis.	*SF*	Sulcus frontalis superior.
L	Lobulus paracentralis.	*SM*	Gyrus supramarginalis.
LP	Lobulus paracentralis.	*SP*	Lobulus parietalis superior.
MT	Sulcus temporalis medianus.	*SPR*	Sulcus subprecunealis.
O	Sulcus olfactorius.	*SR*	Sulcus rostralis.
OD	Sulcus occipitalis diagonalis.	*SRV*	Sulcus rostralis ventralis.
OF	Sulcus orbito-frontalis.	*SRD*	Sulcus rostralis dorsalis.
OI	Sulcus occipitalis inferior.	*SSC*	Sulcus subcalcarinae.
OP	Sulcus opercularis.	*ST*	Sulcus temporalis superior.
OS	Sulcus orbitalis.	*TT*	Gyrus temporalis transversus superior.
PA	Sulcus calloso-marginalis, pars ascendens.		

REFERENCES

Ariens Kappers, C. V. (1929). *The Evolution of the Nervous System in Invertebrates, Vertebrates and Man.* vi + 335 pp. Haarlem: Erven F. Bohn.

Beddard, F. E. (1895). "Contributions to the anatomy of the anthropoid apes." *Trans. zool. Soc. Lond.* vol. xiii, p. 177.

Benham, W. B. (1895). "A description of the cerebral convolutions of the chimpanzee known as 'Sally'." *Quart. J. micr. Sci.* vol. xxxvii, p. 47.

Bischoff, T. L. W. (1870). "Die Grosshirnwindungen des Menschen." *Abh. d. Math. Physik. Cl. d.k.b. Akad. d. Wissensch. Münch.* Bd. x, S. 393.

—— (1877). "Über das Gehirn eines Gorilla und die untere oder dritte Stirnwindung der Affen." *S.B. bayer. Akad. Wiss.* Bd. vii, S. 96.

Broca, P. (1888). "Anatomie comparée du cerveau." In *Mémoires d'anthropologie de Paul Broca,* p. 247. Paris: C. Reinwald.

—— (1888). "Morphologie du cerveau de l'homme et des primates." In *Mémoires d'anthropologie de Paul Broca,* p. 481. Paris: C. Reinwald.

Chapman, H. C. (1879). "On the structure of the chimpanzee." *Proc. Acad. nat. Sci. Philad.* p. 52.

Cunningham, J. D. (1886). "Contribution to the surface anatomy of the cerebral hemispheres." *Roy. Irish Acad. Dublin, Cunningham Memoirs,* vol. vii, p. 1.

Dwight, T. (1895). "Notes on the dissection and brain of the chimpanzee 'Gumbo' (*Troglotides niger*)." *Mem. Boston Soc. nat. Hist.* vol. v, p. 31.

Fischer, E. (1921). "Über die Variationen der Hirnfurchen des Schimpanzen." *Anat. Anz.* Bd. liv (Ergänzungsh.), S. 48.

FLATAU, E. & JACOBSOHN, L. (1899). *Handbuch der Anatomie und vergleichende Anatomie des Centralnervensystems der Säugetiere*, Teil I, 566 S. Berlin: S. Karger.

FULTON, J. F. (1936). "Somatic and autonomic motor functions of the cerebral cortex in ape and man." *Proc. Inst. Med. Chicago*, vol. XI, p. 1.

GIACOMINI, C. (1889). "Sul cervello di un chimpanse." *Atti Accad. Torino*, t. XXIV, p. 798.

GRATIOLET, P. (1850). "Mémoire sur les plis cérébraux de l'homme et des primates." *C.R. Acad. Sci.*, Paris, t. XXXI, p. 366.

HAMY, E. T. (1872). "Contribution à l'étude du développement des lobes cérébraux des primates." *Rev. anthrop.* t. I, p. 425.

HERVÉ, G. (1888). "La circonvolution de Broca chez les primates." *Bull. Soc. Anthrop. Paris*, t. XI, p. 275.

HOLL, M. (1907). "Zur vergleichenden Anatomie des Hinterhauptlappens." *S.B. Akad. Wiss. Wien*, Bd. CXVI, S. 89.

—— (1908 *a*). "Die Insel des Menschen- und Affenhirns in ihrer Beziehung zum Schläfenlappen." *S.B. Akad. Wiss. Wien*, Bd. CXVII, S. 365.

—— (1908 *b*). "Über Furchen und Windungen der Scheitelhinterhauptgegend an den Gehirnen der Affen der neuen Welt." *S.B. Akad. Wiss. Wien*, Bd. CXVII, S. 9.

—— (1908 *c*). "Zur vergleichenden Morphologie der 'vorderen Insel' des menschlichen Gehirns." *S.B. Akad. Wiss. Wien*, Bd. CXVII, S. 325.

MINGAZZINI, G. (1928). "Beitrag zur Morphologie der 'ausseren Grosshirnhemisphärenoberfläche bei den Anthropoiden (Schimpanse und Orang)." *Arch. Psychiat. Nervenkr.* Bd. LXXXV, S. 1.

MÜLLER, J. (1888). "Zur Anatomie des Chimpansegehirns." *Arch. Anthrop.*, Braunschw., Bd. XVII, S. 175.

PANSCH, A. (1868). "Über die typische Anordnung der Furchen und Windungen auf der Grosshirnhemisphären des Menschen und der Affen." *Arch. Anthrop.*, Braunschw., Bd. III, S. 227.

PARKER, A. J. (1896). "Morphology of the cerebral convolutions with special reference to the order of primates." *J. Acad. nat. Sci. Philad.* vol. X (2nd ser.), p. 247.

RETZIUS, G. (1906). *Das Affenhirn*, 66 Il. Jena: G. Fischer.

SMITH, E. G. (1904). "The morphology of the occipital region of the cerebral hemisphere in man and the apes." *Anat. Anz.* Bd. XXIV, S. 436.

TILNEY, F. & RILEY, H. A. (1928). *The Brain from Ape to Man*, vol. II, pp. 447–1120. New York: Paul B. Hoeber.

TURNER, W. (1866). "Notes more especially on the bridging convolutions in the brain of the chimpanzee." *Proc. roy. Soc. Edinb.* vol. V, p. 578.

VROLIK, W. (1841). *Recherches d'anatomie comparée sur le chimpanzé.* 51 pp. Amsterdam: Johannes Müller.

WALDEYER, W. (1895). "Hirnfurchen und Hirnwindungen." *Ergeb. Anat. EntwGesch.* Bd. V, S. 146.

WERNICKE, C. (1876). "Das Urwindungssystem des menschlichen Gehirns." *Arch. Psychiat. Nervenkr.* Bd. VI, S. 298.

ZUCKERKANDL, E. (1908). "Zur Anatomie der Fissura parieto-occipitalis medialis und der Sulcus intraparietalis." *S.B. Akad. Wiss. Wien*, Bd. CXVII, S. 411.

EXPLANATION OF PLATES I–V

PLATE I

Fig. 1. Lateral surface of the right hemisphere of chimpanzee Edith.

Fig. 2. Lateral surface of the right hemisphere of chimpanzee Pau.

PLATE II

Fig. 1. Lateral surface of the right hemisphere of chimpanzee Josephine.

Fig. 2. Lateral surfaces of both hemispheres of chimpanzee Bonzo. Note the differences in cortical markings in the two hemispheres.

PLATE III

Fig. 1. Medial surface of the right hemisphere of chimpanzee Song.

Fig. 2. Medial surfaces of both hemispheres of chimpanzee Bonzo. The variation in the cortical markings of the two hemispheres is apparent.

PLATE IV

Fig. 1. Inferior surfaces of both hemispheres of chimpanzee Bonzo.

Fig. 2. To show the insula and transverse temporal convolutions of the right hemisphere of chimpanzee Bonzo.

PLATE V

Fig. 1. To show the insula and transverse temporal convolutions. Right, chimpanzee Sis, left hemisphere; left, chimpanzee Josephine, left hemisphere.

Fig. 2. To show the bridging convolutions. Chimpanzee Sis, right and left occipital regions.

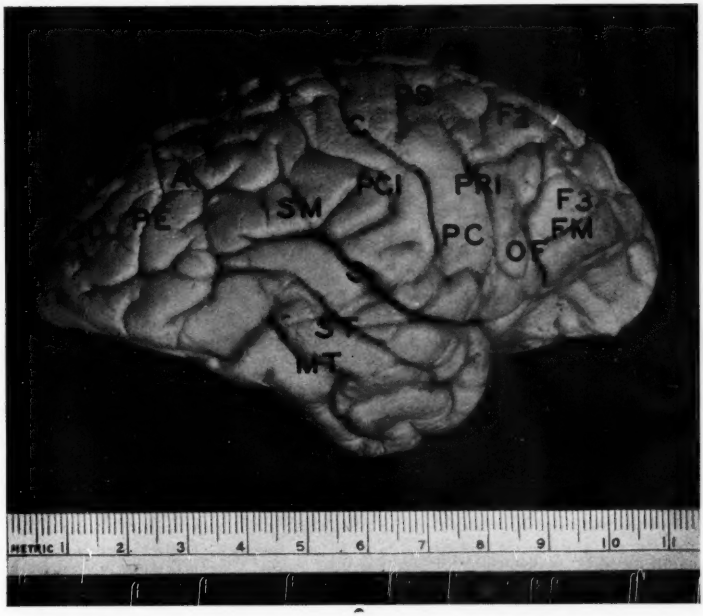


Fig. 1.

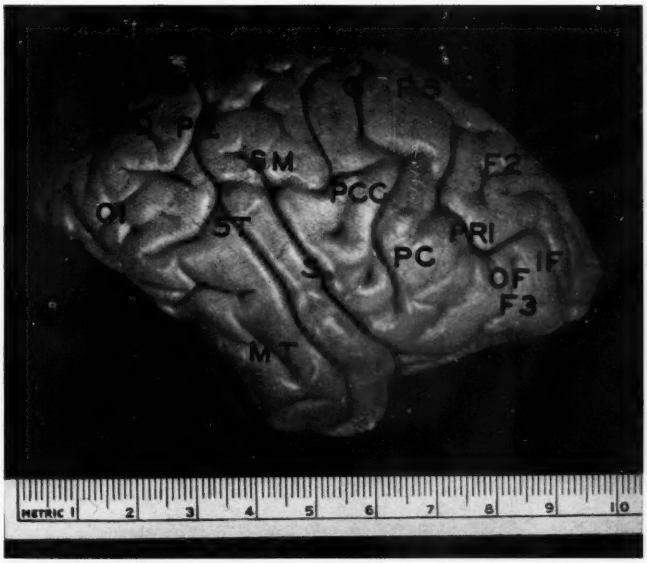


Fig. 2.

UNIV. OF MICH.

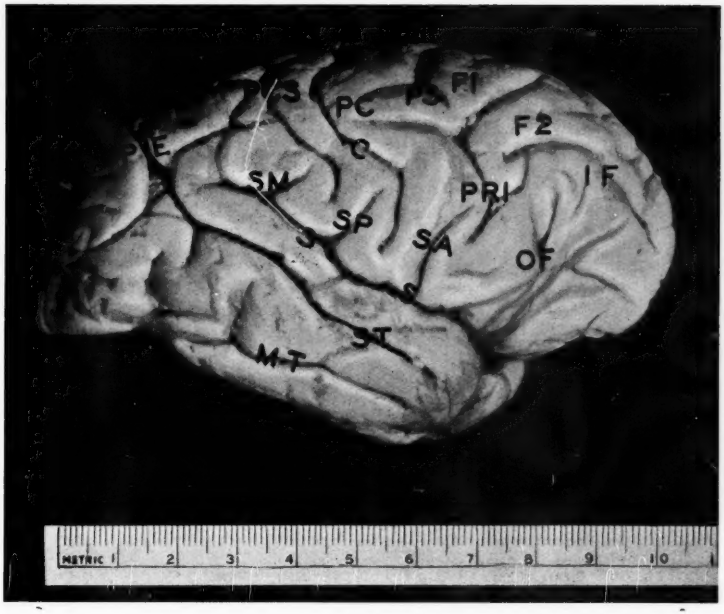


Fig. 1.

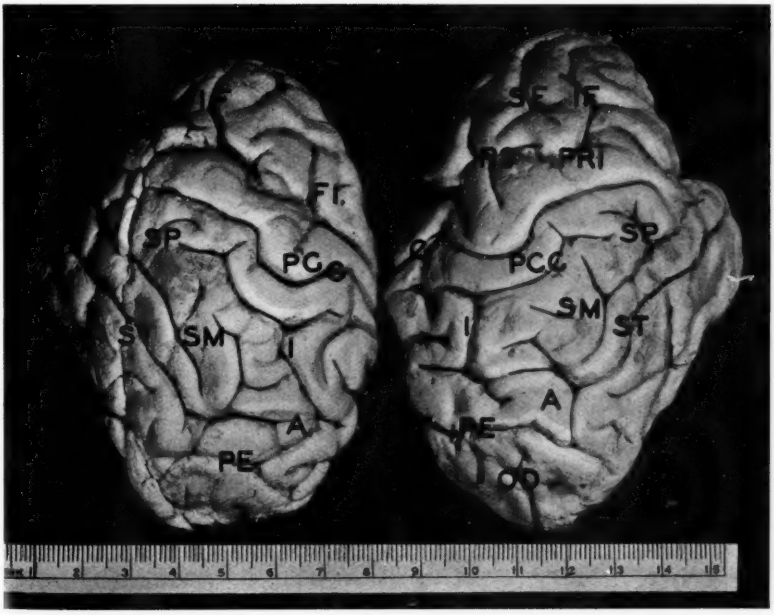


Fig. 2.

UNIV. OF MICH.

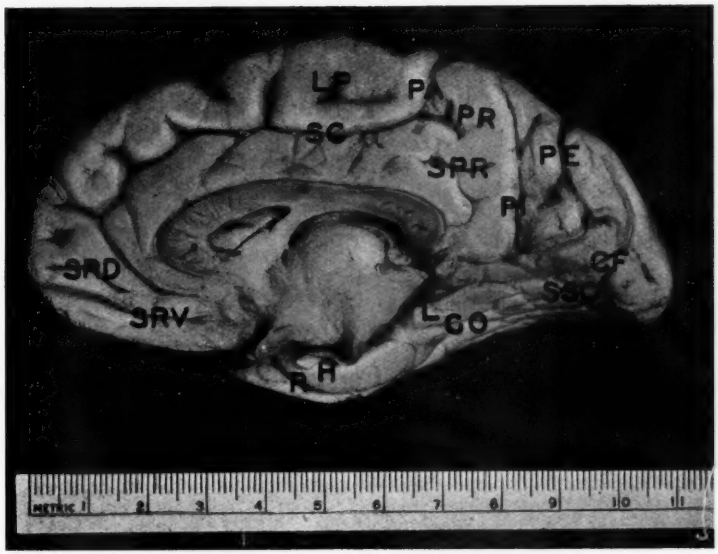


Fig. 1.

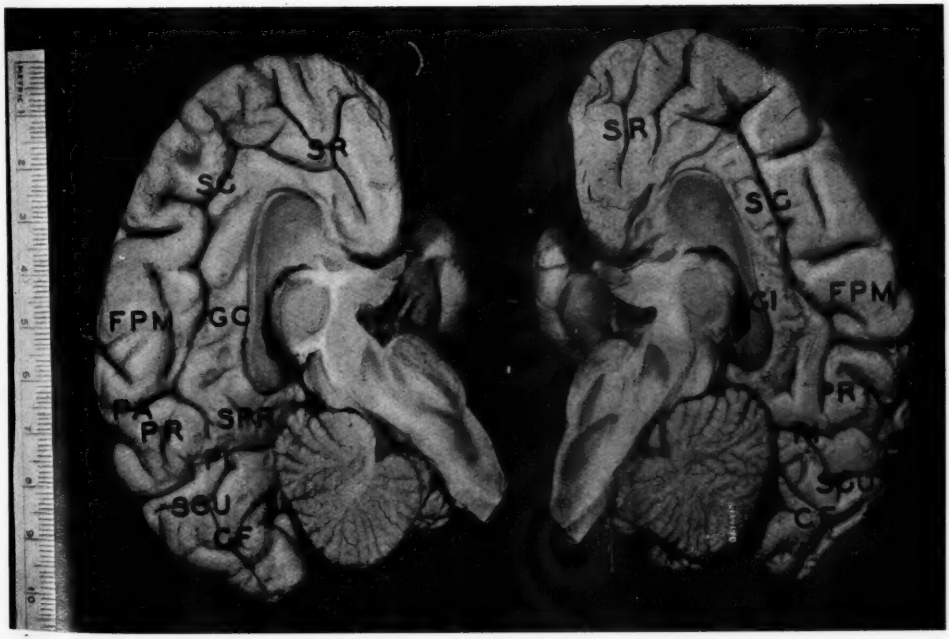


Fig. 2.

UNIV. OF MICH.

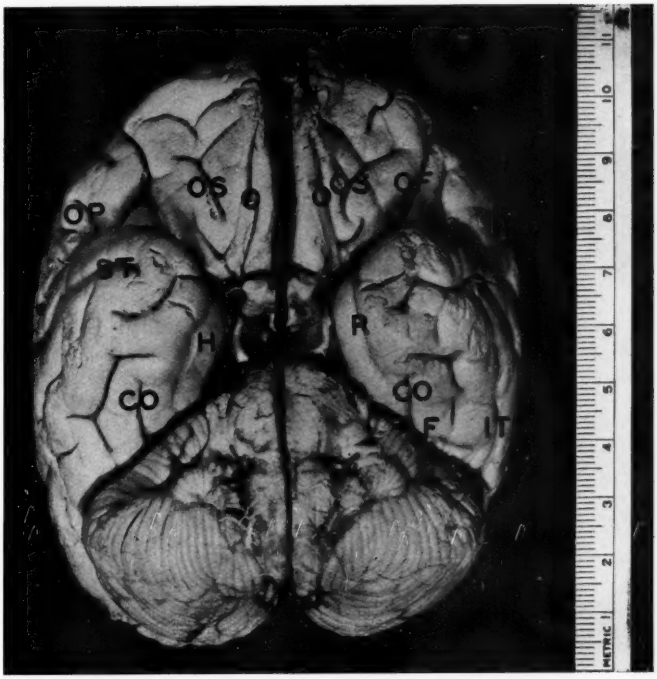


Fig. 1.

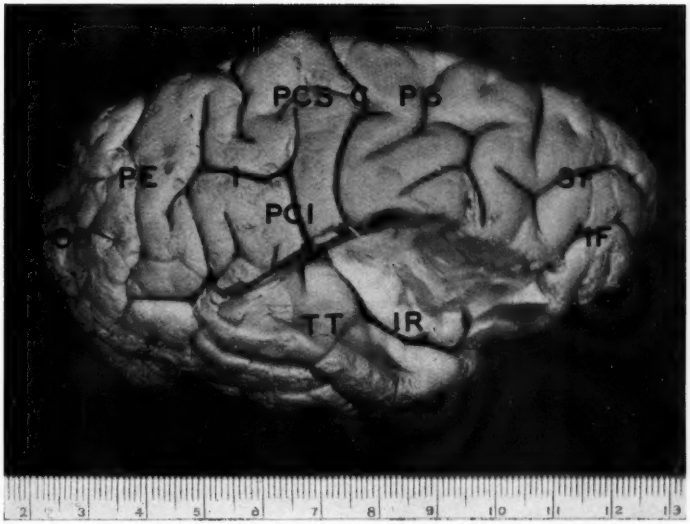


Fig. 2.

UNIV. OF MICH.

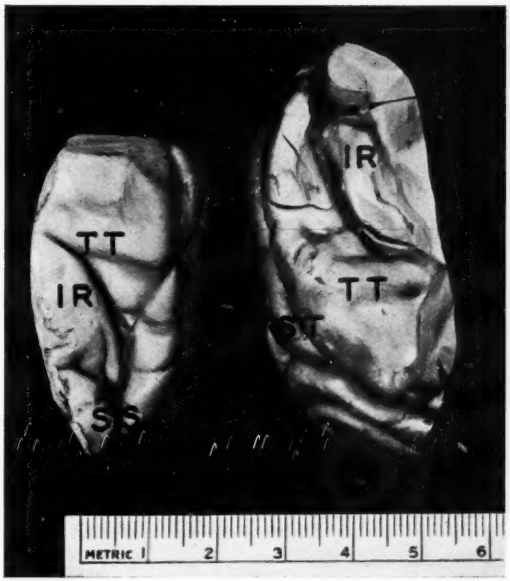


Fig. 1.

Fig. 2.

UNIV. OF MICH.

BLOOD CYSTS IN HUMAN CARDIAC VALVES

By D. RUTHERFORD DOW and W. F. HARPER

Department of Anatomy, University College (University of St Andrews), Dundee

During our investigation of the vascularity of human cardiac valves we observed small dark red nodules on many of the valve cusps of newly born and young infants.

These were of particular interest, as Luschka (12, 14) had described similar nodules in 25 per cent. of hearts examined by him, and these, he stated, were haematomata which had arisen from blood vessels which he claimed existed in normal heart valves.

Their presence has been recorded by several observers. Elsässer (5), who was the first to record them in 1844, found them in more than 50 per cent. of infant hearts between birth and the 23rd day. Parrot (17) examined 120 hearts in the first few months of life, and discovered their presence in 103 of this number. Fahr (6) considered that they occurred almost constantly in the early months of life, that their incidence fell to less than 50 per cent. in the second half of the first year, and that they rarely existed after that age. Their incidence in the first 2 or 3 months was given as 78 per cent. by Haushalter & Thiry (9) and 66 per cent. by Wegelin (18). Jonsson (10) examined seventy-one hearts of premature, stillborn, newborn living and infants. Blood cysts occurred in forty-five of them.

While these statistics indicate that they have been found chiefly in the newborn and in the first few months of life, Bundschuh (3) and Wegelin (19) recorded rare cases in children and adults, and Berti (2) observed them at the sixth month *in utero*.

Most observers agreed that the mitral and tricuspid valves were affected with about equal frequency, and while usually only a few cysts were noted on a valve cusp, in exceptional cases as many as thirty have been seen. Most commonly they are monolocular, but multilocular cysts have been recorded. Only in rare cases have they been found on the aortic and pulmonary valves.

Various opinions have been expressed as to their origin. Luschka (13) considered that they arose as extravasations of blood from vessels which he claimed existed in valves, and in this view he was supported by Parrot (17). Berti (1) was of opinion that there was a vascular regression in valves, and suggested that cysts might arise from blood vessels during this process. Fahr (6) and Hammes (8) accepted this view. Haushalter & Thiry (9) designated them "hématomes" and suggested that they arose by blood being pressed from the cavity of the heart into channels or crevices in the valve, and

Meinhardt (15) and Levinson & Learner (11) corroborated this hypothesis. Nichols (16) also described them as haematomata.

More recently Gross (7) has expressed the opinion that blood cysts were haematomata, and due perhaps to the obliteration of valvular blood vessels.

MATERIAL EXAMINED

The valves of the heart of seven infants up to the age of 6 months were examined microscopically and naked eye, and blood cysts were found in five of the specimens. Those referred to in Table I were observed naked eye as small dark red nodules projecting on the atrial aspects of the cusps a short distance from their edges (Fig. 1). They varied in size from $\frac{1}{3}$ to 1 mm. in

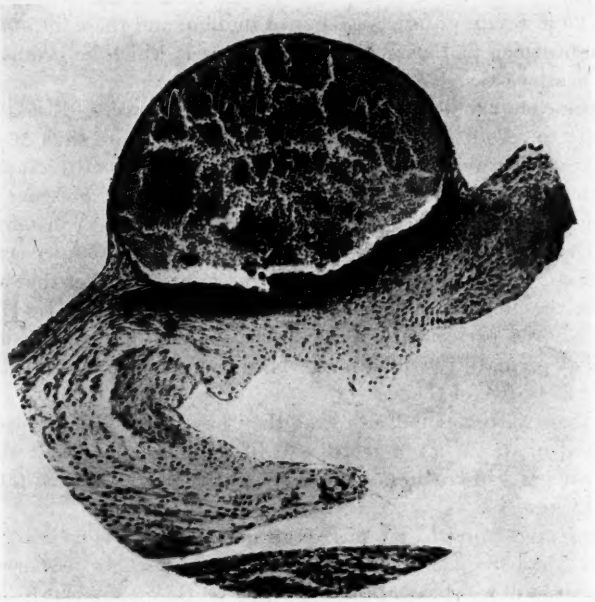


Fig. 1. A blood cyst presenting on the atrial aspect of the posterior cusp of the mitral valve in a female aged 6 days. Diameter slightly less than 1 mm. Erythrocytes and several polymorphonuclear leucocytes are seen within the cyst.

Table I

	Mitral valve		Tricuspid valve		
Sex and age	Aortic C.	Post. C.	Sept. C.	Infund. C.	Marg. C.
Female full-time stillborn	0	1	0	1	0
Female aged 1 day	1	0	0	3	1
Male aged 2 days	0	2	0	0	2
Female aged 6 days	0	3	5	1	2
Female aged 6 months	0	0	2	0	0

diameter, and the elevations produced were smooth with no external opening visible. No. 3 of the series (male aged 2 days) was the only one which revealed cysts microscopically which had not been visible to the naked eye. In this specimen four cysts were found in the posterior cusp of the mitral valve (Fig. 5), and four in the marginal cusp of the tricuspid. With one exception, microscopic examination of the cysts showed that they were monolocular spaces filled with erythrocytes and a few polymorphonuclear leucocytes. Each cyst was lined with a single layer of endothelial cells, while in the case of those

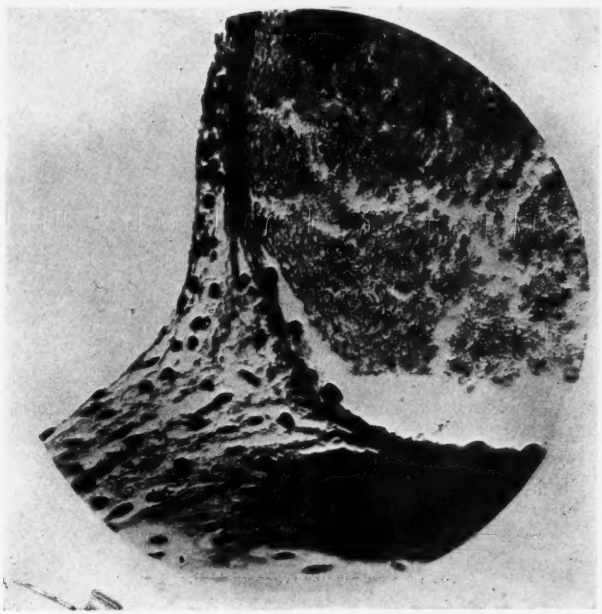


Fig. 2. High-power view of portion of Fig. 1 to show reflection of endothelium from the atrial aspect of the cusp over the projecting part of the cyst.

projecting on the atrial aspect of the cusps an additional outer endothelial covering was also present (Figs. 2 and 3). Our examination revealed that the tricuspid valve was most frequently affected.

ORIGIN OF BLOOD CYSTS

It is now generally accepted that apart from very short extensions of blood vessels into their bases, normal human cardiac valves are avascular. Dow & Harper(4) found from an examination of forty human hearts that this extension of vessels from the line of attachment of the valve to the heart wall

was limited to 3 mm., and was always associated with a prolongation of atrial muscle into the cusp. This condition was present in two of the heart valves in which blood cysts were found, but the latter were situated a considerable distance from the vessels, and it is therefore most unlikely that they result from dilatation of previously existing vessels as others have suggested. We support the view of Haushalter & Thiry that blood cysts originate from the blood in the heart cavity which has been pressed into a valve cusp. In embryonic hearts the traction of the chordae tendineae tends to produce

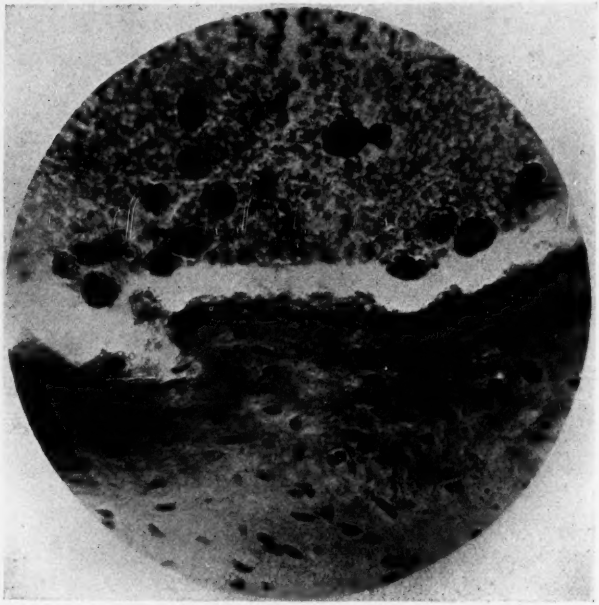


Fig. 3. High-power view of cyst shown in Fig. 1 at junction of cyst and valve cusp. Note erythrocytes and several polymorphonuclear leucocytes.

furrows or undulations in the delicately meshed fibrous structure which has not yet become differentiated into special layers in the cusp, and this is especially marked on the ventricular aspect. We suggest that if fusion of the edges of these furrows occurs, there are formed localized blood cysts which become incorporated in the substance of the cusp. This view is supported by the observation that on serially sectioning the cusps, fusion of the edges of the furrows was seen to be taking place leading to the formation of tunnels of variable size. As the result of traction and pressure these become enclosed spaces which may eventually appear as swellings on the atrial aspect of the cusp. This view is supported by the fact that we noted that each cyst had a

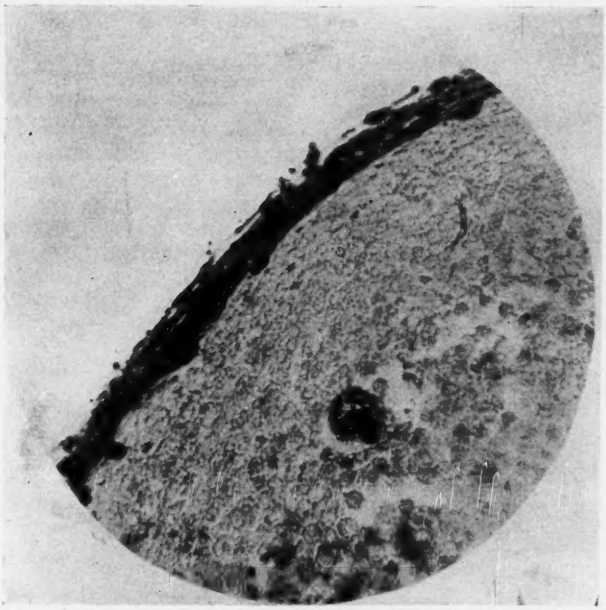


Fig. 4. High-power view of periphery of cyst shown in Fig. 1 to show endothelial walls, erythrocytes in the cavity and a polymorphonuclear leucocyte near the centre of the field.

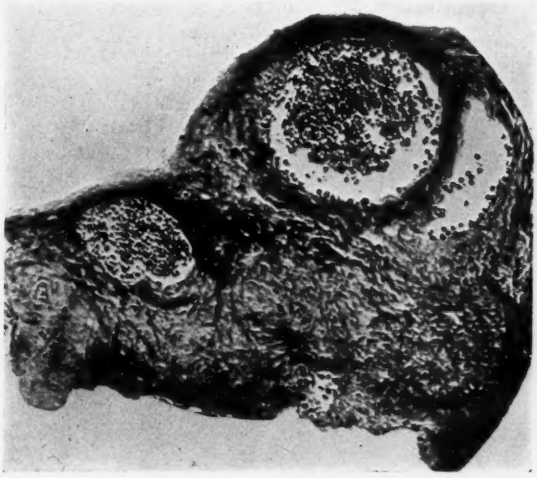


Fig. 5. Longitudinal section of the posterior cusp of the mitral valve in a male aged 2 days in which four blood cysts are present.

complete endothelial wall surrounding it, and that those which presented on the atrial aspect of the cusps acquired an additional layer of atrial endothelium on their projecting surfaces.

Blood cysts do not appear to have any pathological significance, and are a common anatomical finding in the valves of the newborn and infants in the first few months of life.

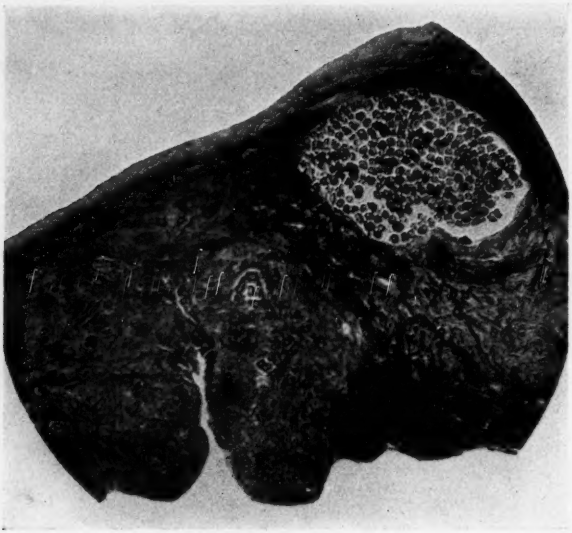


Fig. 6. Distal portion of the cusp shown in Fig. 5, a blood cyst is seen near the atrial aspect and a deep crevice on the ventricular aspect.

SUMMARY

Blood cysts in the heart valves of infants up to 6 months old are described. They occurred near the free edge of avascular valves. We are of opinion that they have arisen from the blood in the heart cavity being pressed into the cusps from the ventricular aspect.

We are indebted to Mr Izzard, technician, for the preparation of the photomicrographs.

REFERENCES

(1) Berti, G. (1898). *Münch. med. Wschr.* Bd. xlv, S. 1194.
(2) —— (1901). *Arch. Kinderheilk.* Bd. xxxi, S. 371.
(3) Bundschuh, E. (1911). *Frankfurt. Z. Path.* Bd. vi, S. 65.
(4) Dow, D. R. & Harper, W. F. (1932). *J. Anat.*, Lond., vol. lxvi, p. 610.
(5) Elsässer, C. (1844). *Med. KorrBl.* Bd. xiv.
(6) Fahr, E. (1906). *Virchows Arch.* Bd. clxxxiv, S. 274.
(7) Gross, L. (1921). *The Blood Supply to the Heart in its Anatomical and Clinical Aspects*, ch. v, p. 53. New York: Paul Hoeber.
(8) Hammes, F. (1908). *Virchows Arch.* Bd. cxciii, S. 238.
(9) Haushalter, P. & Thiry, C. (1898). *Arch. Méd. exp.* t. x, p. 558.
(10) Jonsson, S. (1916). *Virchows Arch.* Bd. ccxxii, S. 345.
(11) Levinson, S. A. & Learner, A. (1932). *Arch. Path. Lab. Med.* vol. xiv, p. 810.
(12) Luschka, H. (1852). *Virchows Arch.* Bd. iv, S. 171.
(13) —— (1857). *Virchows Arch.* Bd. xi, S. 144.
(14) —— (1859). *S.B. Akad. Wiss. Wien*, Bd. lxxxii, S. 498.
(15) Meinhardt, H. (1908). *Virchows Arch.* Bd. cxcii, S. 521.
(16) Nichols, J. L. (1908). *J. exp. Med.* vol. x, p. 368.
(17) Parrot, M. G. (1874). *Arch. Physiol. norm. Path.* t. i, p. 538.
(18) Wegelin, C. (1908). *Frankfurt. Z. Path.* Bd. ii, S. 411.
(19) —— (1912). *Frankfurt. Z. Path.* Bd. ix, S. 97.

ANATOMICAL NOTES

ON THE CARDIAC ARTERIES OF THE ASIATIC ELEPHANT

By A. J. E. CAVE

In a recent issue of this *Journal* Prof. Osman Hill(1) gave a detailed account of the arrangement and distribution of the arteries and veins in the heart of a Ceylonese wild elephant. Remarkably few elephant hearts have so far been studied in detail, whilst available descriptions, where not merely repetitions of former statements, either totally ignore cardiac anatomy, or give at best but an imperfect account thereof. It has been thought advisable, therefore, to place on record this present description of the vascular pattern of an individual elephant heart, partly by way of supplement to Hill's detailed paper, and partly because of certain differences in the vascular arrangements in the hearts of the two animals concerned.

The findings here submitted are those observed in the heart of an adult (but not aged) Asiatic elephant, No. 274 in the Mammal Store of the Royal College of Surgeons Museum. The specimen has been spirit-preserved for some years and its chambers partially dissected: the coronary veins have been in large part removed, so that no description of their arrangement is offered. The contractions due to long preservation largely destroy the value of detailed measurements which are therefore omitted, attention being confined to the course and distribution of the coronary arteries alone.

For brevity's sake it is not proposed to enlarge upon the similarities or differences of arterial distribution in Hill's specimen and the present one. Major differences alone are indicated; for a more detailed comparison of the anatomical findings the two descriptive accounts should be consulted.

General observations

The roots of the great vessels, with the remnants of the fibrous pericardium, remain attached to the heart, whose cavities are exposed. Subepicardial fat is present generally, scanty in amount on the ventricular convexities but abundant in the auriculo-ventricular and interventricular sulci, wherein it completely surrounds and buries the contained coronary vessels. As in Hill's specimen the fat was thick and dense around the pulmonary and aortic roots but ceased at the attachment of the great venous trunks. This superficial fat is of pale yellow tint and firm consistency: the deep fat in the interventricular furrows is brownish and of a looser texture. Between the fat and the exterior of the heart exists a thin, strong investing sheet of condensed areolar tissue.

The aortic trunk, placed dorsal to the pulmonary root, presents three sinuses of Valsalva, disposed so as to correspond with the three cusps of the aortic valve, viz. a right and a left ventrally and a third dorsally. The upper free borders of the aortic cusps lie well below the mouths of the coronary arteries, and it seems highly unlikely that they could ever, in life, have successfully occluded these orifices—a condition which both Hill and Vulpian & Philipeaux(3) regard as at least a probability.

The coronary arteries

Two coronary arteries arise from the aorta, a right and a left, from the respective ventral aortic sinuses. Each at its origin admits the terminal phalanx of the little finger. The left coronary artery has an initial diameter of 16·5 mm., and the right one of 15 mm.: each vessel's wall (in its present contracted state) is 2 mm. or more in thickness.

A. *Left coronary artery*

In the first 2·5 cm. of its course, this vessel is funnel-shaped: it is compressed somewhat against the aortic wall and proceeds between aorta and pulmonary artery to the cranial limit of the left interventricular furrow, where it divides into its terminal interventricular and circumflex branches.

(*a*) *The interventricular branch* descends caudally in the interventricular furrow to terminate at the apex of the heart: during its course it gives off the following branches:

(i) Immediately at its commencement, a moderately large infundibular branch, cut short in this specimen and impossible of further pursuit.

(ii) A similarly sized vessel, from its right aspect, 44 mm. below the preceding, which is distributed to the dorsal aspect of the infundibulum, and to the superficial aspect of the adjacent wall of the right ventricle.

(iii) Three smaller vessels, arising below the preceding at regular intervals, from the right aspect of the interventricular artery, and immediately passing deeply into the substance of the dorsal portion of the right ventricular wall.

(iv) Six large and two small vessels, from its left aspect, which, after a very short visible course in the interventricular furrow, plunge into the substance of the left ventricular wall, and proceeding dorsally therein, ultimately meet and anastomose with corresponding intramural branches from the interventricular branch of the right coronary artery. The most cranial of the larger vessels of this intramural series appears to be distributed to the cranial portion of the interventricular septum.

(v) Terminal branches at the cardiac apex: two or three small vessels, mostly confined to the ventral aspect of the heart, and speedily becoming intramural. Contrary to conditions in Hill's specimen, one precapillary anastomosis at least is evident between one of these terminal twigs and a corresponding apical branch of the right interventricular artery.

(*b*) *The circumflex branch* courses dorsalwards in the left moiety of the coronary sulcus, rapidly diminishing in calibre, and terminating, on the dorsal aspect of the heart (about midway between the left and right interventricular furrows), by anastomosing quite obviously with a vessel from the transverse terminal branch of the right coronary artery. The circumflex artery gives off the following branches:

(i) Four or five small-calibred cephalic arteries which are distributed to the sulcal margins of the left auricle and to the region of the auriculo-ventricular fibrous ring.

(ii) Two fair-sized caudal branches which descend inferiorly from the auriculo-ventricular sulcus and very rapidly enter the substance of the dorsal portion of the left ventricular wall, wherein they probably anastomose with the intramural vessels from the left and right interventricular arteries.

(iii) A number of fine twigs, proceeding from its deep aspect, and passing into the region of the fibrous ring, after supplying the subepicardial fat.

B. *Right coronary artery*

The right coronary artery arises from the right ventral aortic sinus, and is less funnel-shaped than its opposite fellow. It has much the same course as Hill describes, proceeding (between the right auricle dorsally and the infundibulum ventrally, with

the right ventricular wall to its right) to the margin of the last named, around which it sweeps to gain the crux of the heart dorsally, and whereat it divides into its terminal transverse and interventricular branches. It is a longer and a more tortuous vessel than the left coronary. The branches it gives off are (*a*) collateral, (*b*) terminal.

(*a*) *Collateral branches.*

(i) Two vessels arise, one anteriorly, the other posteriorly, from the right coronary immediately after its origin from the aorta. The former descends upon the dorsal aspect of the infundibulum, which it supplies, gives twigs to the fatty tissue, and a (? anastomotic) twig which remains cut short in the specimen. The posterior vessel passes between the aortic root and ventral wall of the right auricle, to supply both these structures with the probable addition of the cranial portion of the interventricular septum.

(ii) Two branches, almost the same size as the preceding, to the cephalic margin of the right ventricular wall.

(iii) Three branches (two medium sized, one small) coursing apically on the right aspect of the right ventricle. After a fairly short course (of about 30–35 mm.) these vessels pierce and enter the ventricular wall.

(iv) Three or four tiny branches pass from the deep (sulcal) aspect of the right coronary, to supply the fat and the caudal aspect of the right auricular wall.

(v) A large atrial (auricular) branch arises from the dorsal aspect of the right coronary, whilst the latter is still under cover of the overhanging right auricular wall. This atrial vessel courses dorsally and to the left, between the aortic trunk medio-ventrally, and the right auricle dorso-laterally, gives twigs to the fat occupying this interval and then expends itself entirely in the supply of the right auricular wall. Contrary to Hill's findings, no atrial artery arises, in this heart, either from the aorta or the left coronary, the vessel here described being the sole auricular artery of any magnitude discovered.

(*b*) *Terminal branches.*

(i) Transverse terminal branch. This continues the general course of the main right coronary artery, running from the crux to the left in the dorsal moiety of the auriculo-ventricular sulcus, wherein, as previously stated, it anastomoses with the circumflex branch of the left coronary. The transverse artery gives off (*a*) three cephalic arteries, (*b*) two caudal branches. The former are short twigs, plunging into the auriculo-ventricular sulcus, supplying the contained fatty tissue, and expending themselves in the caudal margin of the left auricular wall. The latter are larger branches which proceed caudally for some little distance (25–45 mm.) on the dorsal aspect of the left ventricle before sinking into its substance and participating in the general intramural anastomosis. (In Hill's specimen these caudal arteries were derived directly from the interventricular terminal artery.)

(ii) The interventricular terminal branch, much wider and longer than the transverse artery, proceeds in the dorsal interventricular furrow from the crux to the apical notch of the heart. During its course it gives off (α) three or four medium-sized branches from both its right and left aspects for the supply of the contiguous portions of the dorsal walls of the two ventricles, and (β) three or four deep branches, which, arising from its deep aspect, anchor it to the interventricular furrow by piercing the floor thereof, and by passing directly into the thickness of the interventricular septum.

The interventricular artery in this case makes no escape from the interventricular furrow, such as Hill describes, but continues therein to the cardiac apex, where it effects at least one naked eye (if feeble) anastomosis with a vessel from the interventricular branch of the left coronary, as previously noted.

Comments

It is evident that the vascular arterial patterns of the two hearts (Hill's and the present specimen) show a general agreement as to arrangement and distribution of vessels. In some respects, it is true, the latter manifests certain differences—viz. in the greater relative size and distribution of the right coronary artery, in the presence of a small but definite apical anastomosis, and, perhaps, in a more abundant (or, at least, more obvious) septal supply. These differences, however, are no greater than those to be encountered within the limits of individual variation and are therefore of small significance.

The special atrial artery, observed in Hill's specimen to arise directly from the aorta as a third coronary artery, would appear to be of a purely anomalous nature, peculiar to one particular animal and devoid of specific or other significance.

Walmsley(4) in his recent monograph on the heart states that the number of coronary arteries may be increased, in man, to three or even four in number, and quotes Symmers(2) as having detected these small supplementary vessels in 40 out of 100 hearts specifically examined. These additional vessels are regarded as representing normal branches which have acquired an independent aortic origin. Walmsley further comments upon the great numerical inconstancy and the marked variability in pattern of the (human) auricular supply from the coronaries, and finds it impossible to provide any typical description of this distribution.

Apparently the elephant heart manifests this same mammalian vascular imbalance in the matter of auricular arterial pattern, the present specimen exhibiting a particularly large auricular branch of the right coronary and Hill's specimen an anomalous auricular artery of direct aortic origin.

Further conclusions cannot be drawn until additional hearts of this interesting species shall have been critically examined, and the anatomical details published.

It may be added that the cardiac venous arrangements in this present specimen agreed fairly closely, so far as could be determined, with the distributional scheme depicted by Hill.

REFERENCES

(1) Hill, W. C. Osman (1936). *J. Anat.*, Lond., vol. lxx, p. 386.
(2) Symmers, W. St C. (1907). *J. Anat.*, Lond., vol. xli, p. 141.
(3) Vulpian & Philipeaux (1865). *Ann. Sci. nat.* 4e sér. t. v, pp. 183 *et seq.*
(4) Walmsley, T. (1929). *The Heart* (*Quain's Elements of Anatomy*, 11th ed., vol. iv).

AN UNUSUAL OCCIPITO-ATLOID ARTICULATION

By JOHN R. PATE

Anatomy Department, The George Washington University School of Medicine, Washington, D.C.

This note may be of interest because it records an unusual articular arrangement between the occiput and atlas. The subject from which this specimen was secured was a 60-year-old negro female, who apparently had died of tuberculosis of the lungs.

The peculiarity in this instant was in the number and shape of the articulating facets of the occipital condyles and the superior articulating fossae of the atlas. It can be seen (Fig. 1) that there were two distinct facets on each occipital condyle which articulated with two distinct facets of the articular area (the fovea articularis superior) of the atlas (Fig. 2).

Fig. 1. Anomaly of the occipital condyles.

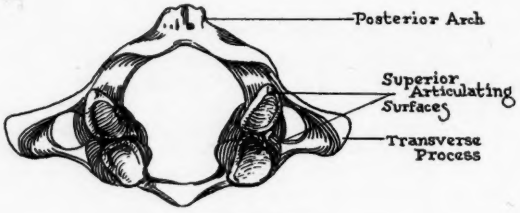


Fig. 2. Atlas.

The usual description found in the standard text-books on human anatomy is that the condyles on the inferior surface of the occipital bone are oval, uniform or elliptical in shape, and the articulating surface is an elongated oval swelling, and that they are convex from before backward and from side to side and look downward and lateralward.

Allen states that the articular surface of the occipital condyles may be composed of two facets of about equal dimensions, an anterior and a posterior, and that these facets may be occasionally separated by transverse grooves. In the description of the superior articulating surface of the atlas it is recorded as being oblong in shape with no mention that there may be two facets on each side. Macalister regarded the superior articular process of the atlas as being formed by "two confluent facets"; however, he does not state that the occipital condyles may also have two facets.

In Gray's text-book of anatomy it is stated that not infrequently the superior articulating surfaces of the atlas are partially subdivided by indentations which encroach upon their margins, but no mention is made of the fact that the articular process of the occipital condyle may likewise be composed of two facets.

All the other text-books consulted state in general that the upper articular processes of the atlas are composed of a large oval facet on each side which is deeply concave with a smooth articular surface which tend to approach each other in front but diverge behind.

Inspection of some one hundred atlas vertebrae revealed only the one described having two distinct articulating facets on each side. Seventy-five per cent. of the superior articulating surfaces of the remaining atlas bones were reniform in shape due to a slight medial indentation about the middle and twenty-four per cent. were of an hour-glass appearance because of a pronounced lateral as well as medial indentation.

The same number of skulls examined resulted in the finding of five specimens which deviated from the normal facets on the left side while the right side appeared as one surface. The fourth specimen had two facets on the right side while the left articulating surface was normal. The fifth had two distinct facets on each side as described and the remaining condyles conformed to the general description.

SUMMARY

A report of an unusual articulating surface of the occipito-atloid articulation.

In conclusion I would like to express thanks to Mr Y. V. Wilcox and Miss Althea Wilcox for their kind assistance.

REFERENCES

(1) ALLEN, HARRISON (1884). *A System of Human Anatomy.*
(2) MACALISTER, A. (1889). *Text-book of Human Anatomy.*
(3) GRAY (1930). *Anatomy of the Human Body*, 22nd ed.

M. CHONDRO-EPITROCHLEARIS BILATERALIS

By I. MACLAREN THOMPSON

Dr Fitzgerald's recent communication in this *Journal* prompts the publication of the following summary of notes of another case, also observed in Montreal; the subject was a white man dissected at McGill University during the session 1923–4.

On the *right* side a round, muscular slip, presenting throughout an approximately uniform diameter of about 5 mm., took fleshy origin from the fifth costal cartilage, between the pectoralis major and the serratus anterior. The first inch or so of the muscle was firmly bound to the inferior border of the pectoralis major by connective tissue, but the two could be separated without cutting muscle fibres. After crossing the axilla, the muscle ended in a fleshy insertion into the deep fascia of the medial side of the arm, mainly into the medial brachial ligament (of Struthers), which was well developed. No blood or nerve supply was observed.

The *left* muscle was a mirror image of that on the right, except that (*a*) it was slightly thicker, (*b*) it arose 1 cm. nearer the mid-ventral line, (*c*) its first inch or thereby was so fused with the inferior border of the pectoralis major that the two could not be separated without cutting muscular tissue, and (*d*) a twig from the lateral thoracic artery entered it (but no nerve supply was found).

On both sides the pectoral muscles were normal. I have no information concerning the history of the person. The differences between this case and Dr Fitzgerald's are obvious upon reading the two papers. In addition to the publications cited by Dr Fitzgerald, Le Double gives an excellent account of the comparative anatomy and the human varieties of the muscle, with many references.

Summary

Brief description of bilateral chondro-epitrochlearis muscle in a white man.

REFERENCES

Fitzgerald, R. R. (1936). "A case showing the chondro-epitrochlearis muscle." *J. Anat.*, Lond., vol. lxx, p. 273.

Le Double, A. F. (1897). *Traité des Variations du Système Musculaire de l'Homme*, t. i, p. 248. Paris: Schleicher Frères.

SOME RARE ABNORMALITIES OF BONES IN THE ANATOMY MUSEUM OF THE GRANT MEDICAL COLLEGE, BOMBAY

By Prof. R. C. MOTWANI, M.B., M.S., F.C.P.S. (Bombay)

(1) Abnormal first rib

The head is flattened vertically, its vertebral edge being thicker above and thinner below. On its postero-lateral aspect is a pentagonal impression for articulation with the body of the first thoracic vertebra. The neck is relatively long, roughly quadrilateral and projects upwards and outwards, with not the slightest backward inclination. The tubercle is transversely elongated with a very small medial articular area. The superior surface in its anterior two-thirds is flattened, looks upwards and outwards, and is more extensive than its posterior one-third, which looks upwards and backwards. At its anterior end is a groove for the subclavian vein which is inclined almost directly backwards. Medial to this groove is a rough area for the attachment of the subclavius muscle. In front of the tubercle is a concave rough area for the attachment of the scalenus medius muscle, and in front of this again is a forwardly directed groove for the subclavian artery. The anterior two-thirds of the outer border of the body of the rib is straight, while the posterior one-third is curved and is marked by the attachment of the serratus anterior. Between the grooves for the vein and artery and abutting on the medial border is a wedge-shaped bony projection. Surmounting this projection is a quadrilateral backwardly directed rough impression for the cartilage of a cervical rib; while anteriorly is a thin raised edge which marks the extensive attachment of the scalenus anterior. Apparently the anterior part of a cervical rib is ossified and fused to the first rib, while the posterior part persisted in a cartilaginous condition. The specimen thus exhibits two features of exceptional interest: (i) the relatively high position of the scalene tubercle, and (ii) the fusion of the ossified anterior part of a cervical rib the posterior part of which was presumably cartilaginous.

(2) Partial lateral fusion of atlas with occipital bone

The atlas appears to be twisted about a vertical axis to such extent that the anterior tubercle is in line with the hamulus of the right medial pterygoid lamina. Compared with the normal, the right half of the anterior arch is relatively short while the left half is elongated. The articular facet for the odontoid process is shifted leftwards and involves the anterior part of the foramen magnum and to a very slight extent the posterior surface of the anterior arch of the atlas.

The right lateral mass lies antero-lateral to the right condyle of the occipital bone. The right inferior articular facet is reniform and slightly concave. The jugular process of the occipital bone and the right superior articular facet of the atlas are partially fused. The left lateral mass and the entire left half of the posterior arch are fused with the lateral condyle and the rim of the foramen magnum postero-laterally. An interval, however, exists for the vertebral artery which grooves the upper surface of the lateral posterior arch in its anterior part, the groove being continuous with the foramen for the vertebral artery entering the foramen magnum behind the left condyle of the occipital bone. The right half of the posterior arch is independent of the occipital bone. The two halves of the posterior arch of the atlas are discontinuous, there being an interval between them.

Fig. 1.

Fig. 2.

Fig. 3.

(3) Anterior fusion of atlas with occipital bone

The anterior arch of the atlas is narrow and completely fused with the anterior margin of the foramen magnum. The anterior tubercle of the anterior arch is trifid and projects inferiorly and to the right. The superior articular facets are fused with the condyles of the occipital bone. The inferior articular facets are flat and not cup shaped. The left transverse process has a foramen transversarium and is distinct from the jugular process, while the right one has no obvious foramen transversarium, is fused with the jugular process laterally and helps to form a foramen between the condyle and the jugular process for the passage of the vertebral artery. The entire posterior arch is partially fused with the posterior margin of the foramen magnum.

RECENT APPOINTMENTS

Prof. H. J. Wilkinson, appointed to the Chair of Anatomy and Dean of the Medical Faculty in the University of Queensland.

Dr W. J. Hamilton, appointed Professor of Anatomy at St Bartholomew's Hospital Medical College.

Dr Archibald Durward, appointed Professor of Anatomy in the University of Leeds.

Dr W. F. Harper, appointed Reader in Anatomy at the London Hospital Medical College.

Dr L. R. Shore, appointed Professor of Anatomy in the University of Hong Kong.

Dr W. A. Fell, appointed Professor of Anatomy in the Medical College, Singapore, Straits Settlements.

Dr R. Wheeler Haines, appointed Assistant Anatomist, St Thomas's Hospital Medical School.

Professor H. H. Woollard has been invited to the Chair of Anatomy at University College, London.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

November 1935 *February* 1936
May 1936 *June* 1936

RECORDED BY
R. J. GLADSTONE

EDITED BY
E. BARCLAY-SMITH

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

NOVEMBER 1935

The Annual Meeting of the Anatomical Society was held at King's College, London, on Friday, 29 November, 1935. The President, Professor FRAZER, in the Chair.

Mr D. STEWART demonstrated a film showing "The action of the calf muscles in the rabbit". The paper will be submitted for publication in the *Journal of Anatomy*. Professor APPLETON, Dr MACCONAILL and Professor WOOLLARD took part in the discussion. Professor APPLETON expressed surprise that the soleus, a red muscle and presumably slow in action, should play such an important part as was shown in the movements of the limb. Mr STEWART, in reply, said it was questionable whether red muscles differed very markedly in function from the white, and suggested that possibly the direct action of the soleus on the ankle joint might account for the very marked change in gait which was observed.

Miss S. GLASSTONE read a paper on "The development of teeth *in vitro*". In reply to questions asked by Professor LE GROS CLARK and Professor WOOLLARD she stated that she hoped to carry out an investigation on the effect of the enamel epithelium on the formation of cusps, and also to study the effect of transplanting it to another part of the body. So far only rat material had been used and this was not suitable for such experiments.

Dr ALFREDA BAKER (with Dr PLATT) demonstrated an abnormal heart. During life there was marked cyanosis. There were no signs of pulmonary disease or bronchial affection. There was marked hypertrophy of the right ventricle. The pulmonary artery appeared to arise from the left ventricle, and the ductus arteriosus was patent. There was no bulbar constriction. In the discussion that followed Professor T. B. JOHNSTON mentioned a similar case in which the child was born dead. Dr MACCONAILL, Professor LOW, Dr CAVE and Dr DURWARD also alluded to cases of "blue baby" which had survived for various periods up to 6 months.

Dr A. DURWARD read a paper on behalf of Dr NORAH SCHUSTER and himself on "An anomalous heart of a child".

The heart was obtained post-mortem from a female child of 6 months. At birth nothing unusual had been noticed, but within a few weeks cyanosis appeared and persisted until death.

The heart is functionally a two-chambered organ. The atrium is incompletely divided into a large right and a diminutive left atrium. There is no significant variation in the venous inlets to either chamber. The septum consists of a poorly developed septum primum in the form of a low crescentic ridge on the posterior wall of the cavity and to the right of this is a stout muscular band crossing the cavity and fusing in front with the septum intermedium. Both

edges of this band are free and on either side of it there is a widely patent interatrial communication.

The A.V. orifices which are guarded by bicuspid valves lie to the right and left of the septum.

The ventricular chamber is large and lacks any muscular septum. Both A.V. orifices lead into it. The outlet is by a large aorta which presents the usual valves and branches and a ductus arteriosus. Leading to the left from this common ventricular character is a narrow channel in the substance of the musculature. It opens with a flattened chamber which is placed, as it were, in the left and anterior wall of the common ventricle. A slender pulmonary artery, with partially fused valves, leads from it, and is connected with the aorta by a patent ductus.

It is suggested that this heart shows the result of arrested development of the bulbus cordis. The small canal which leads from the main ventricle is the ventriculo-bulbar junction and the small cavity into which it opens the bulbus cordis. The absence of a muscular ventricular septum and the variations in the atrial septum are secondary to the bulbar condition.

Mr E. P. STIBBE read a paper on "The disposition of the fibres of the sensory root of the trigeminal nerve".

Giving a summary of the history of the surgical treatment of trigeminal neuralgia, he pointed out that there were now two schools of thought on this matter. British surgery had established, over the last 30 years, a perfect technique of resection of the distal part of the sensory root by the parietal extradural approach. On the other hand Dandy (1925) with numerous followers —some in this country—considered an intradural trans-cerebellar route had many advantages. This method is claimed to be relatively bloodless, much quicker, less dangerous and generally easier than the first method due to Frazier (1901).

These surgical questions scarcely concern anatomy, but Dandy also postulated that there was a rearrangement of the fibres of the Vth nerve in their course from the Gasserian ganglion to the pons—namely that the distal topographic division of the nerve was replaced by a proximal functional segregation of the fibres. Thus the protopathic (spinal root) fibres from all three divisions were to be found in the outer or posterior part of the sensory root close to the pons, and the touch (principal nucleus) fibres in the medial or anterior part of the nerve.

Mr STIBBE had investigated the matter by micro-dissections and by experimental work on monkeys. The results of these dissections show surprising variations but on the whole confirm Dandy's suggestion of the functional segregation of the fibres. The experimental work consists in the comparison of the degenerations produced in the brains of monkeys by proximal and distal resections respectively.

Photographs were shown of nearly complete degeneration of the spinal root resulting from section of the outer half of the nerve close to the pons. Little or no degeneration, however, was found on section just behind the ganglion. Further investigation proved that this was probably due to relatively large nests of ganglionic nerve cells found in the course of the sensory root proximal to the point of section. (These cells have quite recently been also reported by Peters.)

The conclusions so far are that Dandy's claim, that his operation destroys

the spinal root fibres, is justified but that Frazier's operation is uniformly successful with few recurrences, although the existence of the ganglion-cells of the sensory root must render recurrence more likely than after Dandy's operation.

Professor Woollard, Professor Le Gros Clark and Professor Lambert Rogers took part in the discussion.

Mr E. P. Stibbe showed slides illustrating "A specimen of a heart with corrected transposition". This condition has recently been fully discussed by Professor Walmsley. Only some seven or eight cases have been reported and it appears to be an adaptation of the spiral septum of the truncus arteriosus to an abnormal disposition of the developing heart tube, namely that the posterior loop of the heart tube is the right side and the anterior the left.

The special interest of this case lies in the fact that the subject, aged 40, had for many years a pulse of about 40. At least two of the reported cases also had heart-block. This is probably due to a failure of the posterior part of the developing interventricular septum to meet the posterior auriculo-ventricular cushion, the bundle of His thus failing to find its way across this junction. The bundle ends in this case, as it did in Walmsley's case, in a mass of scar tissue between the septal cusp of the tricuspid valve and the interventricular septum.

The histology of the bundle is being investigated and the case may prove to be one of true congenital heart-block.

Professor Davies asked what was the position of the posterior part of the septum inferius, that is whether it had actually fused with the A.V. cushion or not.

Professor Frazer also spoke.

Dr P. Bacsich read a joint paper by Dr A. Gellért and himself on "Museum specimens prepared by paraffin impregnation".

On the basis of previous workers' results (Fréderique, Hochstetter and his school) the authors worked out their own process which enabled them to produce not only preparations of brains and various visceral organs, but also preparations of real anatomical dissections showing clearly the topographic-anatomical relations.

They can formulate their present procedure as follows:

(1) Fixation in 4 per cent (10 : 100) aqueous formalin solution, by injecting through the vessels.

(2) Proceed with the actual dissecting.

(3) Dehydration in 50, 70 and 96 per cent alcohol (the 96 per cent alcohol is mixed with 5 per cent cryst. phenol). For safety a continuous control must be kept over the alcoholic content of the solutions with an alcoholic hydrometer.

(4) 5 per cent cryst. phenol in 2 parts of 96 per cent alcohol and 1 part of petrol.

(5) 5 per cent cryst. phenol in 1 part of 96 per cent alcohol and 2 parts of petrol.

(6) Pure petrol twice changed.

(7) Paraffin of low (36–48° C.) melting point.

(8) Hard paraffin (56° C.).

(9) Hang up preparations for a few hours in incubator to allow the superfluous paraffin to drop off.

(10) Harden preparations at room temperature.

Organs covered with serous membranes or having a smooth rounded surface are practically finished after hardening. Preparations of muscles, nerves and vessels need a smoothing out of their surfaces with a hot iron.

Paint arteries, veins and nerves with different colours and cover preparation with varnish.

The authors believe that the above process completely supersedes the dried anatomical museum specimens and provides preparations which will be of real help in teaching anatomy.

Dr S. ZUCKERMAN read a paper on "Developmental problems of the uterus masculinus".

Mr J. WHILLIS read a paper on the "Action of the tensor palati". He gave an account of movements of the palate as observed by Mr W. E. M. WARDILL and himself in a patient who had been the subject of a wide surgical removal of a rodent ulcer of the cheek. The contents of the orbit and a large part of the maxilla had been removed on the left side, and it was possible to watch the movements from the nasal aspect.

The movements observed during speech were as follows. First the palate is raised into a position in which it is ready for the more mercurial movements of speech itself. Speech movements are extraordinarily rapid and involve nasopharyngeal closure of varying degrees. Movement is greatest in the explosive consonants. In nasopharyngeal closure the salpingopharyngeus contracts first and makes the salpingopharyngeal fold stand out prominently on the lateral wall of the nasopharynx. Immediately after this the synchronous action of the levator palati muscles and of the fibres of the superior constrictor muscle, which produce the ridge of Passavant, brings the palate into apposition with the posterior wall of the pharynx. The two levators and the intermediate part of the palatine aponeurosis act in a slinglike manner rather in the fashion of a digastric muscle, and in addition to elevating the whole palate they raise a marked ridge of mucous membrane on its upper surface. The lifting of the palate by the levator muscles also pushes the salpingopharyngeal fold and the Eustachian cushion upwards and backwards towards the posterior pharyngeal wall. The movements are maximal in blowing, e.g. the inflation of a toy balloon, which necessitates absolute closure of the nasopharyngeal isthmus to prevent the escape of air through the nose.

The action of the tensor palati is not seen during speech but only in deglutition. As the bolus reaches the back of the tongue, grooves appear on each side in the position where the tendons of the tensor muscles enter the palate. The rest of the palate is raised as in speech, which still further accentuates the depressor effect of the tensor muscles. It is suggested that this local depression of the palate squeezes the bolus against the tongue, which at the same time is being drawn back in contact with the hard palate, and that the combined effect is to propel the bolus into the oral pharynx where it is gripped by the constrictor muscles. The nerve supply of the tensor muscle is significant in view of the fact that it is working with the muscles of mastication and of the tongue in this first stage of deglutition.

Replying to a question put by Dr STIBBE, Dr WHILLIS said that, owing to the angle at which observation could be made, it was impossible to state with certainty whether, in the movement of the Eustachian cushion which was noted,

the tube was open or closed. His own impression was that the tube was moved as a whole, and that there was not a movement of the posterior wall alone such as would tend to open the orifice.

Dr D. SHEEHAN read a paper on "Experimental diabetes insipidus". Complete obstruction to the passage of secretion and nerve impulses between the pituitary body and the hypothalamus was accomplished by the application of a silver clip to the pituitary stalk in the dog and the monkey. In the dog there resulted a state of diabetes insipidus whereas in the monkey no polyuria or polydipsia occurred. The canine pituitary showed marked degenerative changes but no comparable changes were demonstrable in the primate pituitary. The explanation of the difference is probably an anatomical one, in the blood supply of the pituitary gland and in the structure of the stalk in the two species. The importance of the close inter-relationship of the pars tuberalis with the tuber cinereum was stressed.

In reply to Professor LE GROS CLARK, Dr SHEEHAN said: We have produced experimental diabetes insipidus in the monkey by lesions placed in the tuber cinereum, posterior to the supra-optic nucleus. The work of Fisher, Ingram and Ranson showed that a lesion involving the supra-optic nucleus bilaterally or its pathway into the tuber cinereum will produce polyuria in cats, but that a lesion anywhere along the supraoptic-hypophyseal tract will result in diabetes insipidus is not supported by our work on monkeys. In reply to Professor WOOLLARD: Fisher, Ingram and Ranson used the stereotactic instrument for making their lesions in the hypothalamus and therefore avoided the danger of injuring the pars tuberalis coincidentally.

Dr M. A. MACCONAILL read a paper on the "Functional anatomy of ligaments". Consideration of the general morphology of the diarthroses suggests that the ligaments are part of the mechanism of the joints for the protection of the joint elements against over-action of shear and torsion forces. They are thus associated in their action with the synovial fluid on the one hand, and with the muscles on the other hand. They have parts to play which resemble both the phasic and the postural roles of the muscles. The carpometacarpal joint of the thumb is taken as an example. The anatomy of its ligaments is deduced from the above principles and is confirmed by dissections.

DEMONSTRATIONS

Professor D. M. BLAIR and Professor F. DAVIES: "Sections of entire heart".

Dr D. M. COOPER: "A vermiform appendix in a macaque monkey". Photographs and sections of an appendicular diverticulum of the caecum from a Rhesus macaque monkey were demonstrated. Since the complete absence of a vermiform appendix is a characteristic feature of the Cercopithecidae, the appearance of an appendicular diverticulum as an anomaly is of some interest. Though superficially resembling an appendix, examination of the sections of the diverticulum failed to reveal any typical aggregations of lymphoid tissue characteristic of a true vermiform appendix.

Dr A. DURWARD and Dr NABANO: "Pancreatic tissue in the wall of a Meckel's diverticulum".

FEBRUARY 1936

An ordinary Meeting of the Society was held at the Middlesex Hospital Medical School, on Friday, 7 February, 1936, the President, Professor FRAZER, in the Chair.

Mr MARCELLI SHAW read a paper on "The vascular path of a thrombus to an orbital arteriovenous aneurysm". Arthur, G., aged 11 years, was brought to me because of an increasing swelling beneath the middle third of the left supra-orbital margin. The diagnosis made was an arterio-venous aneurysm involving the left supra-orbital vein and artery. The clinical history was as follows:

In January 1935 the removal of his tonsils and adenoids was effected by dissection, and eight days later there occurred a right mastoid abscess and this was opened. Three weeks after this second operation, dilated venules were noticed in the left upper eyelid causing a swelling, which has since gradually increased in size and the signs presenting clearly indicate the diagnosis as given, for it can be reasonably assumed, I believe, that a septic thrombus from the site of the mastoid operation had produced the orbital lesion.

The problem was the determination of the pathway of the septic thrombus. It has been suggested a thrombus arising from the right lateral sinus passed via the superior and inferior petrosal sinuses, forward into the right cavernous sinus and thus across into the left, so reaching the superior opthalmic vein.

I am much indebted to Professor Lucas Keene for her valuable opinion that the more probable course was that the thrombus, arising in the right diploic veins, passed through the posterior diploic vein into the anterior, which vessel communicates freely with the diploic vein on the opposite side and in turn effects communication with the left superior orbital vein.

This case serves to illustrate the importance of increasing the clinical recognition of the diploic vascular system.

Dr G. R. DE BEER, on behalf of Professor FELL and himself, read a paper on the "Early development of the skull of Ornithorhynchus". He exhibited a series of model reconstructions illustrating the early development of the cartilaginous and bony skull of Ornithorhynchus. The skull presents a mosaic of features some of which are purely reptilian and others equally purely mammalian. Among the former are the paired trabeculae cranii, the taenia clino-orbitalis, the undivided perilymphaticum and the fused premaxillae with a prenasal process; among the latter, the incus, malleus and stapes, the nasal capsule with its ethmoturbinals and the paired occipital condyles.

The pleuro-centrum of the proatlas (or occipital) vertebra forms the tip of the odontoid process. An alisphenoid bone is present but soon fuses with the basisphenoid. The relations of the "mammalian pterygoid" and "Echidna-pterygoid" suggest strongly that the former represent the detached lateral wing of the parasphenoid and the latter the reptilian pterygoid and the secondary pterygoid cartilage of marsupial and placental mammals.

The paired rudiments of the "dumb-bell bone", or *prevomers*, seem to arise independently of the palatine processes of the premaxillae. Vestiges of prenasal processes of the premaxillae are found in some marsupials (Trichosurus, Caluromys) from which it may be inferred that these forms recently possessed an "egg tooth" and were oviparous.

Professor HILL and Professor WILSON took part in the discussion. Professor HILL said that the paper was one of surpassing interest and would become classical.

Dr A. J. E. CAVE read a paper on "The mammalian odontoid". The odontoid component of the mammalian axis vertebra presents an apex, usually pointed; a head, generally bulbous; a more or less constricted neck; and an expanded basal portion, the cranial aspect of which participates in the formation of the axial articular surface of the lateral atlanto-axial joint. Since however the precise degree of such participation varies considerably in different genera the axial articular surface was studied in immature material in the Museum of the Royal College of Surgeons of England with special reference to this odontoid contribution. Analysis of the findings reveals (descriptively at least) the occurrence of two distinct types of lateral atlanto-axial articulation—Type 1, wherein the odontoid provides the whole of the axial superior articular process, and Type 2, wherein the odontoid element is reduced and the axial neural arch shares in the formation of the process. The second type includes many varying proportions of odontoid to neural arch, as, broadly speaking, the ascent of the mammalian scale is marked by a progressive reduction of the odontoid element in the joint surface and a corresponding increase of the neural component, until in Man and the higher Primates, the odontoid is restricted to the innermost corner of the articular area. Type 1 includes *Ornithorhynchus, Echidna, Macropus rufus, Thylacinus, Sarcophilus, Peragale lagotis, Dasyurus viverrinus, Mustela putorius, Coelogenys paca.* Under Type 2 may be listed *Phascolarctos cinereus, Phascolomys wombat, P. latifrons, Macropus ruficollis, Dendrohyrax, Choloepus, Bradypus, Hydrochoerus, Canis familiaris, C. javanica, C. vulpes, Felis caracal, Hyaena, Phoca, Monachus, Cystophora, Rhinoceros, Equus, Sus, Bos, Ovis, Cervus davidianus, Lemur, Galago, Semnopithecus maurus, Simia satyrus, Anthropopithecus, Gorilla* and *Homo.* Occasionally, in forms listed under Type 2, an additional morphological element intrudes into the constitution of the axis articular facet. This is the not infrequent ossicle (noted in *Lepus, Gorilla, Simia, Homo*) which appears to be the neuro-central epiphysis of the second vertebra and thus to represent the second hypochordal (basiventral) element therein.

An evaluation of the significance of the foregoing data is not easy, from either the schematic or the functional aspect. No precise correlation exists between the grouping into types and accepted classificatory subdivisions of the mammalia, a promising harmony is marred by the inclusion of a carnivore (*Mustela*) and a rodent (*Coelogenys*) in Type 1, and by that of *Phascolarctos* and *Phascolomys* in Type 2. To what extent the odontoid provides the lateral articular surface of the axis vertebra may matter little, and it would be unwise perhaps to attempt to see in the facts of the case anything more significant than mere variation in differing genera and groups of animals.

From the present survey, and on the assumption of a reptilian ancestry of mammalia, the evolution of the lateral atlanto-axial joint emerges clearly. In Theriodonts an occipito-atlantal anarthrosis makes adequate provision for all requisite mobility; herein the occipital condyle articulates with the cup formed by the combined cranial aspects of atlantal centrum (=odontoid), neural arch and hypochordal arch. The odontoid itself remains connected suturally or by ligament with the centrum proper of the axis vertebra: be-

tween these two structures no movement is possible. The bicondylar mammalian occipito-atlantal joint being almost entirely confined to nutatory movements, the necessary provision for the all-important rotation of the skull (and its supporting atlas) is acquired by the development of an articular cavity between the atlantal neural arch (basidorsal) and atlantal centrum (interventral 2). This novel formation—the lateral atlanto-axial joint—is but a functional lateral extension of the more ancient and primitive median atlanto-axial articulation, itself a hypochordo-central (=basiventro-interventral) structure. Thus the joint of Type 1 might be expected to occur, as indeed it does, in Proto- and Meta-theria; but as already hinted the value of this as phylogenetic evidence is doubtful.

It is, however, clear that, descriptively at least, the occurrence of Types 1 and 2 evoke reconsideration of certain accepted homologies in vertebral anatomy. The cervical joints of Luschka (Man, and many Primates) are commonly regarded as of neuro-central position and type, and the lateral atlanto-axial joint is held to be the enlarged homologue of one such articulation, since all lie ventral to their issuing spinal nerve. From a functional viewpoint this interpretation is correct; it is otherwise morphologically. It must be noted that:

(1) The joints of Luschka themselves lie lateral to the neuro-central suture, interposing between successive neural arches (more strictly, between those parts of the vertebral bodies developing from the neural arches). They are therefore intervertebral and interneural.

(2) Between atlas and axis no strictly homologous joint is developed, either in Type 1 or in Type 2.

(3) In Type 2, the lateral part only of the lateral atlanto-axial joint is homologous with Luschka's joints, this part of the joint being both intervertebral and interneural.

(4) In Types 1 and 2 the medial portion of the lateral atlanto-axial joint is an articulation of distinctly different nature. Functionally a lateral extension of the median atlanto-axial joint, it constitutes an *intravertebral* hypochordo-central articulation.

(5) Whilst the lateral atlanto-axial joint of Type 1 may truly be designated "neuro-central", it differs fundamentally from a joint of Luschka in being wholly intravertebral and *not* intervertebral. It is here indeed an articular cavity developed between the components of the temnospondylous first vertebra.

The purport of these observations is to illustrate the supremacy of functional requirements over morphological entity in the elaboration of any special apparatus.

The PRESIDENT commented on the wide range of material examined. Embryologically the increasing superior articular area on the axis spread more and more laterally, encroaching upon and displacing the vertebral artery. He enquired as to the justification for regarding the occasional ossicle in the axis vertebra as hypochordal in nature.

Professor APPLETON held that the variability of sutures invalidated any morphological value which might be attached to them. He cited the great range of sutural pattern in the mammalian acetabulum as an example.

Professor WRIGHT thought that vertebral sutures did demarcate distinct morphological elements and should therefore be accorded significance. He had

always regarded the crossing of an articular surface by a suture (e.g. occipital condyle, atlas, scapular glenoid) as mechanically disadvantageous.

Dr CAVE in reply said that the strictly intervertebral position of the axis ossicle, and its topographical association with the pleurapophysis and neurocentral synchondrosis rendered its hypochordal nature practically certain. Both hypochordal bar and costal element were of basiventral nature. The ossicle itself had been noted by past authors (Toldt, Macalister) but mistaken for the developing rib element.

A transarticular suture was probably advantageous in providing for orderly expansion of an articular area whose growth might be eked out by the appearance of additional ossicles in the suture.

With regard to morphological interpretation of the facts under discussion he returned an open verdict.

Dr JOHN KIRK read a paper on "Voluntary luxation of the shoulder joint by muscular action". He showed a cinema film of a young female, $16\frac{9}{12}$ years of age, who could at will dislocate both shoulder joints by muscular action. The patient was able voluntarily to reduce the dislocation by muscular action. Radiographs were also shown demonstrating the luxation in the subglenoid position.

The muscles chiefly concerned in dislocating the humeral head were found to be the pectoralis major and the latissimus dorsi. The ability to dislocate the joint had been acquired spontaneously without previous injury, and the act had now become so habitual, that when the patient became excited she often jerked the head of the humerus in and out of the glenoid cavity.

A radiograph of the shoulder region in the normal position, with the arm hanging by the side, showed that the head of the humerus occupied less of the glenoid cavity than is the case in the normal individual.

The President, Professor FRAZER, suggested that laxity of the surrounding muscles was the reason for the condition rather than laxity of the capsule as suggested by Dr KIRK.

Professor LOCKHART asked what was the condition of the deltoid muscle during the act of luxation. Dr KIRK replied that the deltoid, although obviously stretched when the humeral head was in the subglenoid position, was relaxed when the dislocation was taking place.

Professor LOCKHART believed that dislocation of the shoulder joint by muscular action was an acquirement possible of attainment by practice in the use of appropriate muscles. In reply to a question, Dr KIRK stated that the individual found no disability, except that the joint sometimes became dislocated in the act of serving at tennis, or in casting the line with a fishing rod. She had to stop momentarily to reduce the displacement before she could go on with her play.

Mr STIBBE read a paper on the "Classification of joints". He criticized the present classification of joints. He considered that the inclusion of symphyses with synchondroses was illogical and misleading to students. The symphyses have much more in common with the synovial joints than with the fixed joints. Mr Stibbe considered that joints should be divided primarily either into joints of movement and joints of growth or perhaps it would be best to fall back on the old form of classification, namely three groups—purely movable, slightly movable and immovable.

Professor BLAIR had written that he was in the main in agreement with this suggestion but thought that the first sterno-chondral joint would be difficult to place, being definitely a synchondrosis and yet movable; but Mr STIBBE thought that it was unnecessary to postulate movement at this joint since the manubrio-gladiolar joint would readily compensate for a rigid thoracic inlet.

Professor WOOLLARD pointed out that Sir Arthur Keith had long ago shown that the movement of inspiration involved a torsion of the first costal cartilage. He also enquired whether this classification was due to the new English nomenclature and suggested that British Anatomists were not necessarily rigidly bound by this nomenclature.

Professor APPLETON pointed out that sutures in the skull could not be regarded as genuine joints of growth.

Professor LE GROS CLARK and Dr JACOBS supported the proposed alteration. The PRESIDENT suggested that the criticisms should be sent to the Standing Committee on Nomenclature.

Mr E. P. STIBBE read a paper on "Hydrocephalus (Haler's case)". He reported further investigations into a case shown by Dr HALER at previous Meetings of this Society—namely the steps taken to decide whether the case was a hydrocephalus or a form of anencephaly. Dissection showed that the thalami, caudate nuclei, fornix and choroid plexuses were all present and that the telencephalon was represented on the right side by a well-marked hippocampus and on the left side apparently by an optic radiation and a small mass of occipital pole. Also it was found possible to turn down a very thin layer from the inner surface of the dura, strongly suggestive of a very attenuated cerebral cortex. These points suggested that the case was one of congenital hydrocephalus and this was confirmed by histological examination of the "cortex" when, after prolonged search, a single, very large pyramidal cell characteristic of cortex was found. The point of special interest in the case, which may be accepted as one of hydrocephalus, lay in the fact that the skull and the dilated brain had grown just to normal full-time foetal size.

Professor FRAZER asked if the evidence was sufficient to exclude anencephaly. Professor LE GROS CLARK thought that the evidence definitely proved hydrocephalus. Professor WOOLLARD commented on the case as a good illustration of the independence of the growth of the skull. Professor ROGERS asked if the aqueduct and the fourth ventricle had been examined. Mr STIBBE replied to these points.

It is hoped to complete the investigation of the case and to publish a full report in the *Journal of Anatomy*.

Dr R. H. ROBBINS read a paper on "Abnormal azygos veins".

Dr JOHN KIRK read a paper entitled "Observations on the plica inguinalis, gubernaculum and associated structures in rabbit and marsupial embryos".

Dr J. KIRK made a grateful acknowledgement to Professor J. P. HILL who had provided the material upon which the observations had been made, and explained that the present communication incorporated some of the work done on the same subject by his brother, Dr E. W. KIRK of Hong Kong, when at University College in 1925–6.

Lantern slides were shown demonstrating the following subjects:

(1) Posterior abdominal wall of early rabbit embryos showing the mesonephros and associated structures, with sex still undifferentiated.

(2) Abdominal cavity of early rabbit embryos, of both sexes, showing size and attachments of the plica inguinalis.

(3) Microphotographs of abdominal wall of early rabbit embryos showing stages in the formation of the plica and conus inguinalis, and the relation of these structures to the primary gubernacular strand.

(4) Microphotographs of the inguinal region in rabbit, marsupial and human embryos showing the position of the primary strand.

(5) Microphotographs of the inguinal region in marsupial embryos showing how the early formation of the processus vaginalis separates the primary strand into two zones, a central core and a peripheral sheath.

Observations

A. *Formation of the plica inguinalis*

The mesonephros in its early condition extends caudally to the hinder end of the abdominal cavity and is attached along its whole length to the abdominal wall by a short, thick mesentery.

As the mesonephros and wall recede from each other, this mesentery lengthens and the bays of the coelom on each side of it enlarge and deepen, reducing its thickness until only a thin fold of mesenchyme attaches the mesonephros to the abdominal wall. As the caudal pole of the mesonephros recedes from the wall, the hinder part of the fold is drawn out into an attenuated band (plica inguinalis) which stretches from the tubar portion of the mesonephros to a spot on the abdominal wall immediately lateral to the umbilical artery. The latter attachment becomes cone-shaped (conus inguinalis of Klaatsch 1890) and is situated just medial to the anterior limit of the differentiating sheet of lateral abdominal muscles and just lateral to the lateral edge of the developing rectus abdominis muscle.

B. *Changes in the conus and plica*

Stage 1. *Formation of the primary strand.* The mesenchyme in the centre of the conus and plica becomes markedly condensed and forms a strand extending from the tubar attachment of the plica cranially to the base of the conus caudally where it is closely associated with the anterior edge of the transversus abdominis muscle. Before any muscle fibres are discernible in this condensation strand itself, it is seen to extend distally into the abdominal wall, penetrating the lines of the internal and external oblique muscles whose fibres are already clearly differentiated. This penetration continues until the strand reaches the scrotal primordium in which lymph spaces (lymphatic spaces of Berry Hart 1908–9) are clearly seen. At this stage the strand is found lying between two well-defined sheets of developing muscle, the transversus, internal and external oblique on its lateral side and the rectus on its medial side. Further, it is evident that this condensation band (gubernacular strand) reaches the scrotal primordium before any evagination of the coelom (processus vaginalis) at the base of the conus has taken place.

Keisselbach in a recent account of his researches into Descensus Testiculorum in Didelphys (1934) has described this condensation strand and calls it the "primarstrang". He defines it as "a strand of condensed connective tissue which passes as the continuation of the abdominal plica inguinalis from

the site of origin of the processus vaginalis towards the scrotum and, in the female, towards the hinder mammary primordia".

It is clear that this is the same structure which Cleland found in the human embryo (1856), calling it the "gubernacular cord", and which Keith similarly described in 1923.

Stage 2. *Formation of the processus vaginalis and its relation to the primary strand.* The coelom is now seen to dip into the abdominal wall surrounding the base of the conus and to extend caudalwards into the substance of the condensation strand. Consequently this extension of the coelom into the abdominal wall (process vaginalis peritonei) is found splitting the strand into two zones, a central core and a peripheral sheath, separated from each other by the space of the processus except dorsally where they are attached by a thin mesentery. The core of the strand becomes the gubernaculum of descriptive anatomy while the peripheral part of it becomes the cremaster muscle.

C. *Nature of the primary strand*

When the strand first appears its cells are very similar in appearance to those found in the condensation seen in the caudal part of the mesonephros itself.

The strand apparently first forms within the substance of the plica and, to begin with, the cells are congregated in its anterior part. Striped muscle fibres soon appear in the strand and our observations suggest that these originate within the plica itself rather than that they migrate into it from the abdominal musculature.

The fibres of the transversus abdominis are closely associated with the base of the conus but it is not clear that they extend up into the conus itself. This point requires further investigation.

D. *Further fate of the primary strand*

The muscle fibres found in the core of the strand become the muscle of the gubernaculum testis: those differentiated in the peripheral zone become the cremaster muscle.

The lateral abdominal muscles are at first distinct from this but as their fibres stream ventrally and caudally they mingle with the fibres of the cremaster and become the coverings of the testis and spermatic cord when, at a later date, these take the place of the gubernaculum within the sac of the processus vaginalis.

MAY 1936

An ordinary Meeting of the Society was held in the Anatomy Department of St Bartholomew's Hospital Medical College, on 15 May, 1936, the President, Professor FRAZER, in the Chair.

Dr J. WHILLIS, on behalf of Professor R. B. GREEN and himself, demonstrated, with the aid of a film, a "Case of ectopica cordis". In reply to a question by the PRESIDENT he stated that he had not regarded the fold alluded to as the right venous valve, because of its relation to the superior vena cava. Professor WATERSTON enquired what was the cause of death, which Dr Whillis said was most probably pericarditis. To a question by Professor DAVIES,

regarding the presence of atrio-ventricular nodal tissue, the author stated that histological examination for nerve cells would be undertaken.

Dr A. R. PARKES read a paper on "A relation of the sciatic nerve". The relation described was a fascial band, which could be displayed by raising the pyriformis muscle. In two cases of sciatica the pain had been relieved by division of the band. Professor WATERSTON enquired whether the band was not of the nature of a muscular aponeurosis, rather than a simple fibrous band. The PRESIDENT remarked that normally the gluteus minimus and pyriformis muscles are very closely associated, and Professor WRIGHT stated that morphologically the pyriformis muscle is a portion of the gluteal sheet which has migrated into the pelvis. Professor APPLETON stated that in the Okapi an extensive aponeurotic sheet is perforated by the sciatic nerve, and that there is a long extension of the gluteus minimus muscle under the sciatic nerve.

Professor WOOLLARD gave a short descriptive account of the new Anatomy Building of St Bartholomew's Hospital.

Professor H. WOOLLARD read a paper on "Intraepidermal nerve-endings". Professor WATERSTON, in discussing the paper, referred to experimental evidence which indicated that the epidermis was insensitive to pain, pain only occurring when the deeper subepidermal tissues were injured.

Mr D. STEWART stated that in his work with Dr LEVINSKY on the periodontal membrane of the cat, they found the thick fibres terminated in end-organs, while the fine fibres tended to break up into still finer fibres.

Dr J. O. W. BLAND gave a cinematograph demonstration, devised by R. G. CANTI, J. O. W. BLAND and DOROTHY S. RUSSELL, of "Tissue culture of gliomata". Migration of tumour cells is shown in examples of astrocytoma, oligodendroglioma and spongioblastoma multiforme. In astrocytoma the cells are of elongated bipolar form and move slowly with relatively little alteration in shape.

In oligodendroglioma the cells are more mobile and retain the polygonal form and delicate branching processes characteristic of their appearance in histological sections. They also exhibit curious pulsating movements and tend to collect into clumps.

In spongioblastoma multiforme the migrating tumour cells in general resemble those of the astrocytoma. They are, however, more mobile and more plastic. The present example, cultured for 6 weeks, shows a predominance of spindle cells in the early stages of culture, while stellate cells, indistinguishable from astrocytes, predominate in the later stages. During the first few days the cultures show large numbers of macrophages which are not seen later. Dark ground illumination show filamentous mitochondria in the tumour cells in both astrocytoma and spongioblastoma multiforme. Mitosis is also shown in both tumours; in spongioblastoma multiforme it is demonstrated on the 42nd day of culture.

The film as a whole demonstrates the individual character of astrocytes and oligodendroglial cells; also a close similarity between the examples of astrocytoma and spongioblastoma multiforme.

Professor W. E. LE GROS CLARK read a paper on "The thalamic connexions of the temporal lobe".

Dr E. Henrietta Jebens demonstrated "A bony specimen of the artificially deformed foot of a Chinese woman". The specimen is a skeleton of the foot of a Chinese woman showing the result of the ancient custom of foot-binding.

The origin of the custom is so sunk in antiquity that it is to-day impossible to discover how it originated. It was already practised in the sixth century B.C. and many theories have been brought forward to explain whence it arose, but none have been proved.

The manipulation of the feet is usually begun between 5 and 7 years of age and sometimes as early as 3. The deformity is produced in two stages. The first stage consists in the flexion of the four outer toes and their gradual rotation beneath the plantar surface of the foot. In this way the big toe remains straight and the foot becomes shaped like an acute-angled triangle with the base at the heel and the apex at the big toe. In this manipulation the metatarso-phalangeal and inter-phalangeal joints are mostly dislocated and often the delicate phalanges and metatarsals of the child are fractured. After many months or a year during which time the feet are kept firmly bound in this position the second part of the manipulation is begun. This consists in approximating the anterior and posterior parts of the foot, using the heel as a "point d'appui". This results in a tilting upwards of the anterior part of the os calcis so that the axis of this bone is almost vertical instead of horizontal. The astragalus becomes pushed up and together with the scaphoid and cuneiforms form a very high arch resting on the os calcis behind and on the head of the 1st metatarsal in front, and producing a deep furrow on the plantar aspect of the foot. These features are well shown in the specimen. The antero-posterior length of the foot, after binding, is often not more than 5 in. long when the bandages are on but will lengthen out to 6 or 7 in. when the latter are removed. After the deformity is once well established it is well-nigh impossible to reduce it and many women are unable to walk at all without the support of a bandage. They walk on their heels, using the forefoot as a buttress to assist in maintaining their balance.

Dr S. Zuckerman read a joint paper by J. Z. Young and himself on "The course of fibres in the dorsal roots of Rhesus monkey".

Professor Woollard read a joint paper by Mr J. H. Gray and himself on "The lymphatic vessels of the skin".

Dr P. N. B. Odgers described a specimen of an "Early human *in situ*".

Professor J. Beattie read a paper on "Afferent fibres of the great splanchnic nerve". Professor Woollard, Dr Zuckerman and Dr Boyd took part in the discussion.

JUNE 1936

The Summer Meeting of the Society was held in the Anatomy Department, Marischal College, Aberdeen, on 26 and 27 June, 1936. The President, Professor J. Frazer, in the Chair.

A joint paper by F. H. Bentley and Miss M. Hill on the "Repair of divided nerves and fate of nerve grafts" was read by Miss Hill. The paper was discussed by the President, Professor Woollard, Professor Davies and Professor Waterston. Miss Hill in reply to Professor Waterston said that

it made very little difference in the speed of regeneration whether the nerve was simply divided or crushed. She also stated that degeneration might take place in an upward direction for a distance corresponding to the intervals between two nodes of Ranvier.

Dr G. G. LENNON read a paper on the "Stages in the life-history of the basophil cells of the hypophysis cerebri". The basophil cell of the pars intermedia is developed from the cells lining the posterior wall of Rathke's cleft, and as it travels into the neural lobe it enlarges and develops deep blue-staining granules until, at the height of its maturity, it lies in the region of the gland known as the pars intermedia and appears to be almost bursting with these granules. As it travels still further into the neural lobe this basophil cell undergoes degeneration by one of two methods, apocrine or holocrine, and when entirely degenerated it represents the hyaline body of Herring. These bodies can be traced into the blood vessels of the neural lobe, and similar bodies are found in the hypophysio-portal vessels of the pars tuberalis.

The basophil cell of the anterior lobe develops from the chromophobe cell by enlarging and by accumulation of granules. It pours out its secretion, but does not degenerate.

Photographs were shown of the various stages.

DISCUSSION

Professor FRAZER remarked that he did not agree that the development of the pars intermedia is by an inversion from the posterior wall of Rathke's cleft as he had quite often seen such inversions in sections of foetal hypophyses which he had examined.

In view of recent work published, Dr BOYD suggested that the route of the secretion of the posterior lobe is in a direction opposite to that described, viz. that the flow in the hypophysio-portal vessels of the pars tuberalis is downwards, and that the hyaline bodies are artefacts. Dr LENNON, in reply, said that the hyaline bodies are far too constantly present to be artefacts, and that since the posterior lobe of the hypophysis is the only source of the secretion the route taken by it in the hypophysio-portal vessels could only be upwards.

Professor WOOLLARD asked the source of the material studied and was informed that all Dr Lennon's sections were from human hypophyses.

Dr F. GOLDBY read a paper on the "Olfactory and thalamic connexions of the reptilian forebrain". Professor WOOLLARD and Professor BEATTIE took part in the discussion.

Professor WOOLLARD read a paper on "Heat spots". Professor WATERSTON and Professor BEATTIE took part in the discussion.

Professor BEATTIE read a paper on "Further evidence for the existence of a parasympathetic centre in the hypothalamus". Experimental evidence of the existence, in the pre-optic and supra-optic areas of the hypothalamus, of a zone which on electrical stimulation give rise to increased motor activity of the stomach and bladder. The area was well defined and it was found possible to trace its projection tracts posteriorly into the upper mid-brain. These tracts lay in the periventricular network and eventually reached the zone of white

matter immediately dorsal to the dorsal grey matter surrounding the Sylvian aqueduct. This work was carried out in collaboration with Dr A. S. KERR.

Dr P. BACSICH, on behalf of himself and Mr E. P. STIBBE, read a paper on "A neuro-histological problem". In studying the histology of lesions of the central nervous system of experimental animals, and more especially of pathological conditions in man, it has until now been necessary to decide in advance whether the method to be used shall be a silver impregnation, toluidin blue, or Weigert staining. This is because, as is well known, each of these methods requires not only a special treatment but also as a general rule a special fixation, after which there is no possibility of interchange as between the different techniques.

The possibilty of being able to use simultaneously the three main techniques of neuro-histology on neighbouring sections of the same material has interested many investigators, and many attempts have been made to solve the problem —e.g. the Landau technique for the staining of the medullary sheath on unmordanted celloidin sections; or the Roger, Foot and Davenport silver impregnations on slides. Up to the present, however, no satisfactory method has been evolved, and this weakness in our microtechnical armament forced us to re-attack the question. Our special objective was as follows: (1) ordinary formalin fixation; (2) paraffin or colloidin-paraffin embedding; and (3) no special treatment before the section is fixed on the slide.

As the slides will show, such a treatment has now been devised, and the slides include silver, Weigert and toluidin blue preparations from the same block.

It is felt that the present results want confirmation and careful checking before they are available in their final form for the use of laboratory technicians; therefore it is not proposed to give details of the technique at this stage, but only to put on record that such a method has been evolved, and to show the results.

Meanwhile the following comments are added:

(1) This is not so much a new technique as a composite one, abstracted and modified from the large number of techniques already available in the literature.

(2) It is believed that the method will make it quite unnecessary to predecide the technique. One can simply make a paraffin or celloidin-paraffin block, and cut and stain the sections as required.

(3) The ordinary Weigert treatment makes the material very brittle, and therefore it is not particularly good for serial sectioning, either in celloidin or in paraffin embedding.

(4) Silver impregnation in bulk rarely gives uniformly-stained sections, as the peripheral part is too dark, and the central part is too weakly stained; the intermediate part only can therefore be used for observations able to withstand criticism.

(5) All the mordanting as well as the staining is done on the slide, and is a matter of hours instead of days or even weeks, as in block staining.

(6) Even if the material was easily available—(experimental animals)—in order to compare differently stained sections more than one animal was necessary; and therefore it was obviously impossible to guarantee that the sections for comparison were cut at the same level, or even in the same plane.

It is further specially to be noticed that in human pathology, in most cases one subject and one piece of material alone are available, consequently the ability to use various techniques on the same block would strengthen our diagnosis remarkably.

Dr M. A. MacConaill, on behalf of Professor F. Davies and himself, read a paper on "Cor biloculare and the development of the pulmonary veins". The President and Professor Blair discussed certain points bearing on the anomaly with respect to the origin of the pulmonary veins from a subintestinal vein, and the relation of the bundle of His to the septum inferius.

Professor Brash read a paper on the "Anatomical problems in the Ruxton case". He showed lantern slides illustrating anatomical evidence given in the case of Rex *v.* Ruxton, with particular reference to the anatomical problems in the assembly of the mutilated bodies, and to the use of photographic superimpositions of skulls and portraits in helping to establish the identity of the two murdered victims.

Professor Learmouth read a paper on "The innervation of the lower end of the ureter". He said that his paper was a plea for the clinical importance of detailed anatomical study. The lower end of the ureter had a nerve of its own, arising from the hypogastric ganglion. It could be reached by direct dissection, or it could be inactivated by division of the hypogastric nerve (or presacral nerve if both sides were to be interrupted). This nerve appeared to control the tone of the uretero-vesical orifice; its inactivation was of use in cases of idiopathic dilatation of the ureter, the operation resulting in free drainage of the dilated duct. A series of five cases in which the operation had been carried out was described, and the results assessed. These varied with the stage at which the operation was undertaken and the results were best when the musculature of the ureter had not been destroyed by the chronic inflammatory process which was an invariable feature of stasis.

In reply to Professor Davies he said that he had not personally examined the lower end of the ureter for ganglion cells in its wall.

Dr J. F. Philip read a paper on "A slight variation in the posterior surface of the calcaneum". Frequently there occurs an increased projection backwards and upwards of the bursal area on the posterior surface of the calcaneum, and this results in an increase in size of the angle formed between the posterior and inferior surfaces of the bone. The average size of the angle in normal conditions appears to be between 63° and 68°, whereas in those cases with a prow-like projection of the bursal area the angle is in the region of 75° or over, sometimes as high as 85°. This increase in size is easily demonstrable in lateral radiograms of the heel.

The variation described is the cause of a painful swelling in the heel, frequently met with in young women, just proximal to the insertion of the tendon and is produced as the result of pressure and friction between the bone, the tendon and the upper margin of the back part of the shoe. In some cases where a painful swelling of the tissues exists in this situation, no abnormality of the calcaneum is demonstrable radiologically and such cases are the result of badly-fitting shoes and obtain permanent relief by

(1) simple excision of the subcutaneous adventitious bursa to which the presence of the swelling is due, and

(2) lowering the level of the upper margin of the back part of the shoe.

In the type of case where an increased upward and backward projection of the bone can be demonstrated radiologically, recurrence inevitably follows the above procedure, as the fault does not lie primarily in the type of shoes worn. To obtain permanent relief in this type, the projecting bursal area must be removed at the same time, and this is easily done by a posterior approach dividing the central part only of the tendon and so leaving intact the strongly lateral expansions which sweep on to the medial and lateral surfaces of the bone. By this device one gets a much better exposure for the even removal of the bursal area than is obtained by a lateral approach, and at the same time any permanent weakening of the tendon is avoided.

Dr PHILIP made replies to the following questions:

(1) To Professor FRAZER who asked if a wedge resection of the upper surface would not be better than the method described, "Any disturbance of this part of the bone in the nature of a fracture is very difficult to treat, always resulting in persistent pain lasting for months and so much bone would have to be removed that the condition would be analogous to a fracture".

(2) To the suggestion of a lateral approach, "This would almost certainly lead to uneven removal of bone leaving a sharp razor-like edge on the distal part".

(3) Is the condition found only in people with acrocyanosis? "No, it usually occurs in healthy people but repeated attacks of inflammation occur, especially during cold weather".

(4) Is there any weakening of the tendon? "The lateral expansions remain undisturbed and they are powerful enough after suture of the divided central part to prevent weakening". Dr STEWART, who gave a communication on the recovery of the tendo calcaneus after division, corroborated this.

Mr D. STEWART, on behalf of Dr LEVINSKY and himself, read a paper on the "End-organs of the periodontal membrane".

Dr M. A. MACCONAILL showed a cartoon film (animated diagram) of "The development of the female genital tract". The picture consists of 400 ft. of sub-standard (16 mm.) film. It follows the course of development from the stage of the pronephros to that just preceding birth. The film is designed to supplement the usual methods of teaching, and emphasis is laid upon the chief dynamic features of the process, controversial points of detail being avoided as far as possible. Copies of the film are available.

Mr D. STEWART read a paper on the "Repair of tendons". In this investigation a series of three rabbits was used. The sheaths of the superficial flexor muscles were exposed in both hind limbs immediately above the heel. These were then opened and $\frac{1}{2}$ in. of the enclosed tendons was resected. The deep flexors were next exposed and divided. The wound was closed and the animals received no further treatment. During the next six weeks they were kept in a large room in which they could move about freely. The alterations in the gait of the animals were studied by means of cine films taken at the rate of 64 frames per second. The film was shown to the Society and demonstrated that, immediately after the operation, the animals' gait became fully plantigrade and remained in this condition for three weeks. After this period, there was a steady and rapid improvement in the method of locomotion, the animals

becoming more and more digitigrade, and at the end of six weeks, the gait was practically the same as in the normal animal before operation. After this, the animals were killed and post-mortem examinations made at the site of operation. It was found that the gap between the ends of the tendons had been filled in by strong bands which closely resembled tendon in naked eye appearance. There was a definite shortening in the length of the muscle bellies. The skin was freely movable over these tendinous bands and they did not adhere to the neighbouring structures. Celloidin embedded histological preparations were made of the newly-formed tissue. Microscopical examination showed that the newly-formed tissue resembled normal tendon in its structure, differing from it only in the following points:

(1) The tendon cells were less flattened.
(2) The strands of fibre separating the layers of cells were thinner.
(3) The tendon strands had a more wavy appearance.

Dr G. I. Boyd showed an "Anomalous heart", obtained at post-mortem from a child aged 3, who died of pneumonia (Dr Polson's case, St James' Hospital, Leeds). The viscera were transposed but the heart showed only partial transposition, a condition which has been referred to by Maude Abbott under the title "Incomplete Heterotaxy" (*Osler's Modern Medicine*, 3rd ed. 1927, IV. p. 664).

The atria were not marked off from one another. The left half of the common atrium was structurally similar to a normal right atrium and received the inferior vena cava and a left superior vena cava. The right half of the common atrium received the pulmonary veins and an additional (right) superior vena cava. The cardiac veins opened directly into the atrium. The two halves of the common atrium were therefore structurally and functionally transposed. In the ventricles the transposition was imcomplete for the right ventricle which gave origin to the aorta and functioned as a left ventricle had all the appearances of a right ventricle. The left ventricle, too, was structurally not transposed, but gave rise to the pulmonary trunk and a patent ductus arteriosus. In association with this functional transposition of the ventricles the septum of the truncus arteriosus has developed in such a way that the ascending aorta passed in front of the pulmonary trunk and there was an aneurysmal bulging of the membranous part of the interventricular septum into the upper (vestibular) part of the left ventricle.

Professor Frazer agreed that the ventricles showed incomplete transposition, but could not account for all the anomalies in the atrial part of the heart. Professor Davies drew attention to the fact that the veins of the heart ended directly in the common atrial chamber. Dr Boyd said that this was so because the horn of the sinus venosus which normally developed into the coronary sinus had in this case become the additional (right) superior vena cava. In answer to Dr MacConaill, Dr Boyd said that a persistent additional (left) superior vena cava opening into the left atrium as well as into the right atrium had been described by McCotter (*Anat. Record*, 1916, p. 373).

Dr Boyd also demonstrated a case of "Abnormal origin of the right common iliac artery", which was given off from an enlarged third lumbar artery on the right side, and was continued downward in the Psoas major muscle, as an intersegmental anastomosis, into the ilio-lumbar artery of the same side. The President agreed with the opinion expressed by Dr Boyd regarding the

origin of the anomaly, and commented on the frequency of the production of abnormal vessels by the enlargement of normal anastomoses.

Dr L. R. Shore read a paper on "Interparietal groove". He showed some ancient Egyptian skulls with an external interparietal groove lying between two ridges.

Professor Brash discussed the mechanism of changes in form which are produced by the deposit of subperiosteal bone on the outer side and absorption of bone from the inner side. Professor Blair alluded to a variation in the contour of the skull, produced by an unusual arrangement of the fibres of the occipito-frontalis muscle and its aponeurosis, in which a postfrontal groove was associated with a thickened transverse band due to fusion of longitudinal fibres of the aponeurosis, the groove being apparently due to pressure-atrophy of the bone lying beneath the band.

Professor D. R. Dow read a paper on "Two cases of anomalous intestinal rotation".

Case 1 was a male aged 4 years and 5 months. The first part of the duodenum was normal in position, relations, and fixation. The second part of the duodenum passed vertically downwards in relation to the anterior aspect of the right kidney and its vessels. There was no mesoduodenum. The third part of the duodenum was directed to the left for a short distance anterior to the superior mesenteric vessels, then turned sharply downwards and to the right. The suspensory ligament of the duodenum was poorly developed. The jejunum occupied the right iliac fossa and was related to the under surface of the liver which was enlarged as the result of severe fatty degeneration. The ileum was situated mainly in the pelvis, and its terminal part passed from right to left to enter the caecum. Together with the jejunum it was suspended by a narrow mesentery which was attached to the posterior abdominal wall. Around this narrow pedicle, complete rotation of jejunum and ileum had occurred in a clockwise direction through 360°, and obstruction had developed at the junction of duodenum and jejunum.

The caecum lay in the left iliac fossa with its posterior surface directed anteriorly. The ascending colon passed upwards and to the left, and formed the hepatic flexure to the left of the middle line. Together with the caecum it had a mesentery continuous with that of the jejunum and ileum. The transverse colon continued to the right, formed an angular bend, from which it passed to the left, and lay at first in relation to the greater curvature of the stomach, then behind it to reach the lower border of the pancreas having formed a loop convex downwards; it terminated in the left colic flexure. From the under surface of the liver and gall bladder a well-marked broad band of peritoneum (hepato-cysto-colic ligament) crossed the first part of the duodenum to be attached to the angular bend on the transverse colon, which was further stabilised by peritoneal bands which connected it to the anterior surface of the second part of the duodenum. Around this fixed point the ascending colon and caecum could be freely rotated. The descending colon was normally disposed against the posterior abdominal wall.

Case 2 was a male aged 38 years. The radiograms of this patient showed that the jejunum and ileum lay in the right lumbar and iliac regions, and in the pelvis. The ascending colon was situated to the left of the middle line, and

the right colic flexture lay below the transverse colon. The radiographic appearances were confirmed at an operation.

Comments. The two specimens described were due to incomplete rotation of the mid-gut loop, but it was not possible to state the cause of this. There was no evidence to suggest that the condition was due to lack of development of "retention bands" obvious at the 35 mm. stage, and described by Frazer as essential for complete rotation to occur. The abnormally developed peritoneal bands between the transverse colon and adjacent viscera in case 1 were secondary adhesions which had arisen during the process of fixation, and were in no way responsible for the abnormality. Approximately fifty cases of gross displacement of structures developed from the mid-gut loop have been recorded, and minor degrees of it are common.

Dr J. D. Boyd read a paper on the "Nerve supply to the branchial arch arteries of vertebrates". The position of specialized pressor-receptor areas in mammals can be explained on the assumption that they are developed in relation to persisting portions of the branchial arch arteries. With the exception of the work of Nonidez and Muratori on avian material little has been published on the pressor-receptor areas in infra-mammalian vertebrates. Gills of Mustelus treated with reduced silver techniques show a rich supply from the branchial nerves to the branchial arch arteries, especially to the point of junction of the efferent branchial arterioles with the efferent arteries. It is suggested that this neuro-vascular relationship may be the anatomical basis of the pressor-reflexes described in elasmobranch branchial arch arteries by Lutz and Wyman. This suggestion is strengthened by the work of Irving, Solandt and Solandt who have recorded action currents synchronous with the heart beat from all the true branchial arch nerves of the dog-fish. A similar mechanism is found in the branchial arteries of perennibranchiate amphibia. In amphibia, which undergo metamorphosis, terminations of the glossopharyngeal nerve can be found in the carotid labyrinth (a structure developed in the walls of an anastomosis between the afferent and efferent limbs of the larval third arch artery) and in the adjacent portions of the carotid arch artery. Pressor reflexes can be elicited from the carotid labyrinth. In reptiles nerve-endings suggestive of a pressor-receptor function are present in the third arch artery but no physiological proof of their function has been obtained. In reptiles there is the first definite appearance of cells resembling those of the mammalian carotid body and related, as this structure is, to segments of arteries which possess a specialized afferent nerve supply.

It is suggested that the evolutionary stages of the carotid body—carotid sinus complex of vertebrates are: (1) a basic stage, such as is found in Mustelus, in which afferent branches of the branchial nerves terminate as free-endings in relation with the adventitia of the branchial arch arteries. At this stage there are no "paraganglionic" cells. The nerve fibres are pressor-receptor in function and there is no evidence for a specialized chemo-receptor apparatus. (2) A stage such as is found in those amphibia which undergo metamorphosis. There is a specialized portion of the commencement of the internal carotid artery supplied by fibres from the glossopharyngeal nerve and having a pressor-receptor function, and, as yet, no definite evidence for a chemo-receptor function. (3) The stage which is found in amniotes; here the commencement of the internal carotid artery has a specialized pressor-receptor mechanism

consisting of fibres from the glossopharyngeal nerve which terminate in complex arborescences in its adventitia. The carotid body is, in the later stages of mammalian development, separate from the wall of the internal carotid artery; it possesses a complex afferent nerve supply (chiefly from the glossopharyngeal) which is probably chemo-receptor in function. A similar interpretation may eventually be given for those carotid-body-like structures which are related to the aorta and the pulmonary artery of mammals. Whatever the phylogenetic explanation may be, however, it seems justifiable to conclude that the branchial arch arteries of vertebrates, whether functional or the transient vessels of embryonic development—from which, in higher types, the adult arterial pattern is derived—are sites of election for the development of pressor-receptor mechanisms. Further, in the amniotes these vessels and their pressor-receptor nerve-supply have associated with them cellular condensations (the carotid body and the paraganglia, associated with the aorta and the root of the pulmonary artery) which are intimately related in their development to the corresponding artery and its afferent nerve supply.

In reply to Professor WOOLLARD, Dr BOYD said that the carotid body and the homologous structures in the thorax were much more closely related, in their development, to the cranial nerves than to the sympathetic but he did not consider that the evidence for the production of acetyl-choline (or other anti-adrenalin substance) was impressive.

In reply to Professor BEATTIE, who asked if there was any similarity between the cells of the carotid body and certain cells of the central nervous system which have an endocrine appearance, Dr BOYD said that, while the cells of the carotid body had some features suggesting active secretion, their relationship to nerve-endings that are afferent in appearance and the physiological work of Heymans and others are much more suggestive of an afferent function. In his opinion the cells are comparable to the cells of taste buds. He has never seen, in the carotid body, inclusions of colloid material such as have been described by Scharrer in the paraventricular and supraoptic nuclei (Scharrer's "Zwischenhirndrüse").

Professor D. M. BLAIR showed photographs, on behalf of Mr JAMES FLEMING, of "a case of proboscis unilateralis" in a male infant. The nose externally was normal on the right side but flattened on the left, and the left nostril was represented by a short, blind pit. A "proboscis" hung downwards from an attachment between the root of the nose and the left medial canthus; this was tunnelled by a mucus-secreting canal which opened at the lower end of the proboscis but seemed to end blindly in a slight dilatation at the upper, attached end of the process. Fluid injected up this canal failed to reach the left conjunctival sac. The right nasal fossa seemed normal, save that its medial wall was deflected to the left. Only one posterior naris could be detected, and radiographic examination revealed a single, narrow nasal fossa apparently in the median plane of the head. Near the medial end of the left lower eyelid was a notch with a punctum lacrimale on each side of it; fluid injected into these puncta could not be made to flow elsewhere.

Dr G. M. WYBURN read a paper on "The development of the infra-umbilical abdominal wall". In reply to a question asked by the PRESIDENT, Dr WYBURN said that he regarded the failure of the mesoderm to obliterate the allantoic

portion of the cloacal membrane as probably due to a deficiency of the processes of mesoderm, normally arising from the caudal end of the primitive streak, and passing round the cloacal membrane, to fuse with the downgrowth of mesoderm from the body stalk. He suggested that epispadias was due to a minor mesodermal error in development.

Dr C. P. MARTIN showed some "Radiograms of movements of the shoulder joint". He referred to his previous communication to the effect that when the arms are brought into a vertically upright attitude the position of the humerus is always exactly the same, no matter whether the arms have been brought to the upright attitude by flexion or abduction, and the uniformity in the position of the humerus when the arms are vertically upright is due to the fact that during abduction of the arms the humerus rotates laterally through almost 90°. The radiograms were those of a boy aged 9 with the upper epiphyseal line showing very clearly, and by means of the prominences on this line the lateral rotation of the humerus during abduction of the arm could be clearly demonstrated. A further interesting point was that the lateral end of the clavicle rose during abduction of the arm until the limb was approximately at right angles to the body, but as the arm was elevated further towards the upright attitude the outer end of the clavicle fell. Radiograms of adults, kindly lent by Professors Lockhart and Brash, were also shown which confirmed these points.

Professor LOCKHART denied that the position of the humerus when the arm was brought into a vertically upright attitude by abduction was identical with its position when the arm was brought to the same position by flexion. He showed several radiograms in support of his argument. But he admitted that during abduction of the arm lateral rotation of the humerus did occur but not, he thought, to so great an extent as 90°. Several other speakers also discussed the communication.

Dr MARTIN in reply stated that Professor LOCKHART'S radiograms were invalidated as one arm only had been abducted. In such cases it was quite possible to abduct the arm to a considerable extent and by tilting the thorax at the same time carry the arm vertically upright without much rotation of the humerus. But these were not cases of true abduction. Tilting of the thorax should be prevented by raising both arms together and then full lateral rotation of the humerus always occurred if the arms were carried to the fully upright attitude. In radiograms, particularly those of adults, it is often difficult to demonstrate rotation of the humerus. Noting the position of the epicondyles at the lower end of the humerus was really a better guide for rotation than the use of radiograms and by this method the rotation of the humerus could be clearly demonstrated.

Professor LOCKHART, while agreeing that external rotation of the humerus might occur during elevation of the arm, did not consider that it was invariably essential during abduction from the position selected for anatomical description, and demonstrated this, using the flexed forearm as a pointer indicating the absence of rotation. He considered that mobility depended mainly upon muscular action, and that practice would considerably increase the scope in the great majority of subjects, and showed a photograph of Mr Naughton Dunn's case, in which a patient with arthrodesis of the shoulder joint could elevate the arm by scapular rotation only almost to the erect position.

He further disagreed that the terminal position of the structures was the same, whether the arm was raised by flexion or by abduction, and showed X-rays, in which the great tuberosity pointed mainly laterally, and mainly medially, when elevated by these two methods respectively. He did not agree with Dr Martin's contention that there was enough tilting of the thorax in these X-rays to account for the discrepancy in their opinions, and agreed to secure X-rays of the shoulder joint when both arms are raised (and tilting of the thorax thereby prevented) by flexion and also abduction, to elucidate the point still further.

Professor LOCKHART also showed, as a matter of interest in this connexion, X-rays of the shoulder joint with the arm erect in the extremes of lateral and medial rotation, which demonstrated that in this position the amount of possible rotation of the humerus, however achieved, was at least 180° in certain subjects. He expressed his indebtedness to Dr BRAILSFORD for the radiographs.

DEMONSTRATIONS

Dr W. F. HARPER and Dr D. WILSON: "The blood supply of the ureter".

Professor R. D. LOCKHART:

(1) "X-rays of the diaphragm in various postures of the subject during inspiration and expiration". No appreciable difference was found in the level of the diaphragm in the standing and sitting positions. It lies approximately at the lower border of the 11th thoracic vertebra during inspiration, and at the lower border of the 9th thoracic vertebra during expiration, in either position. Lying on the back, in inspiration, the diaphragm reaches the upper border of the 10th thoracic vertebra, and in expiration, the lower border of the 8th thoracic vertebra. When the subject lies on one side, or stands with a bend to one side, the diaphragm on that side, particularly in expiration, reaches a level from 1 to 1½ vertebrae higher than on the opposite side, while the costo-diaphragmatic recess becomes narrow on the first-mentioned side, and wider and shallower on the other. When the abdominal muscles are so contracted as to produce a surface concavity, the diaphragm is caused to ascend, almost to the extent of two vertebrae, either during inspiration or expiration.

(2) X-rays, photographs and footprints of adult feet, (1) arched, (2) relaxed, (3) superimposed tracings of (1) and (2), showing the mobility of the arches, (4) standing on the toes, (5) in extreme plantar flexion, (6) inverted, (7) on the points in a ballet dancer (with photographs and radiographs of the slipper worn at the time), were shown. Attention was drawn to the position of the sesamoid bones in the big toe; and to the extended position of the great toe, the flexed position of the lesser toes, and the occurrence of callosities upon the lesser toes, due to pressure upon the toe-cap in the ballet-dancer's foot.

BRAIN PREPARATIONS

BY MEANS OF DEFIBRILLATION OR BLUNT DISSECTION

By J. W. HULTKRANTZ

Professor of Anatomy, University of Uppsala, Sweden

10s. 6d. *net*

"The method of blunt dissection or defibrillation as applied to the study of the brain has long been practised at the Anatomical Institute, Uppsala, in the teaching of students. Prof. Hultkrantz has here briefly described the procedure with the help of a series of excellent photographs of dissections obtained....It might well be used effectively for museum preparations as well as in the dissecting room." LANCET

"The author does not claim that the splitting method has any special advantage in elucidating scientific problems in the nervous system. He can justly claim, however, that as a medium for teaching important anatomical facts it is excellent." IRISH JOURNAL OF MEDICAL SCIENCE

"It will make a special appeal to teachers of anatomy, and to those students who are dissecting the brain a second time." ST THOMAS'S HOSPITAL GAZETTE

"We can confidently recommend it to those teaching anatomy and to those in charge of anatomical museums who are not yet conversant with the advantages of dissections made in this manner." GLASGOW MEDICAL JOURNAL

WILLIAM HEINEMANN (MEDICAL BOOKS) LTD

99 GREAT RUSSELL STREET, LONDON, W.C. 1

Statistical Studies in Genetics and Human Inheritance

ANNALS OF EUGENICS

Edited by R. A. FISHER

Founded by K. PEARSON

Vol. VII, Part II will contain articles by

R. A. FISHER — L. McMULLEN

F. YATES — A. S. WIENER *et al.*

M. N. KARN — S. BARBACKI

I. ZIEVE *et al.*

Subscription, in advance, 50s. per volume

Four quarterly parts, obtainable separately at 15s. each, from

THE GALTON LABORATORY

UNIVERSITY COLLEGE, GOWER ST., LONDON, W.C.1

CONTENTS OF PART 1

VOLUME LXXI

PAGE

SIR GRAFTON ELLIOT SMITH. A Biographical Sketch of his Earlier Career (with Portrait as frontispiece) 3

W. E. LE GROS CLARK. The Termination of Ascending Tracts in the Thalamus of the Macaque Monkey (with 11 Text-figures) 7

R. ANTHONY et J. DE GRZYBOWSKI. Le [illegible] du Mouton—Etude de son Développement et Interprétation de ses [illegible] (avec 31 figures dans le texte) 41

H. H. WOOLLARD. Intra-Epidermal Nerve Endings (with 1 Text-figure and Plates I–III) 54

C. U. ARIËNS KAPPERS. The Endocranial Casts of the Ehringsdorf and *Homo soloensis* Skulls (with 7 Text-figures) 61

N. GOORMAGHTIGH. On the Existence of Abdominal Renal Paraganglia in the Adult Mouse (with 2 Text-figures and Plates I and II) 77

M. H. BOOK. The Secreting Area of the Glomerulus (with 2 Text-figures) 91

W. LEWINSKY and D. STEWART. The Innervation of the Epidermal Membrane (with 3 Text-figures and Plate I) 98

K. J. FRANKLIN, D.M., M.R.C.P. and A. D. McLACHLIN, M.D., M.Sc. The Uterine Vein Valves in the Rabbit (with 2 Text-figures) 103

A. EARL WALKER, M.D. and JOHN F. FULTON, M.D. The Synergal Configuration of the Cerebral Hemispheres of the Chimpanzee (with Plates I to V) . . 105

D. RUTHERFORD DOW and W. F. HARPER. Blood Cysts in Human Cardiac Valves (with 6 Text-figures) 117

ANATOMICAL NOTES. On the Cardiac Arteries of the Asiatic Elephant. By A. J. E. CAVE 124

An Unusual Occipito-Atloid Articulation (with 2 Text-figures). By JOHN R. PATE 128

M. Chondro-Epitrochlearis Bilateralis. By I. MACLAREN THOMSON 130

Some Rare Abnormalities of Bones in the Anatomy Museum of the Grant Medical College, Bombay (with 3 Text-figures). By Prof. R. C. MARWARI, M.B., M.S., F.C.P.S. (Bombay) 131

RECENT APPOINTMENTS 134

PROCEEDINGS 135

INSTRUCTIONS TO CONTRIBUTORS

1. Manuscripts should be typewritten or written in very legible hand and must be fully corrected. Contributors will be responsible for the payment of any sum charged for the correction of the printer's proof in excess of ten per cent. (16 pages).

2. Illustrations must be in a finished form ready for reproduction. They must be properly lettered or labelled in type or by hand with reference numbers if necessary.

3. Line drawings must be sent whenever possible. Illustrations requiring half-tone blocks are very costly and the results are often unsatisfactory.

4. The legend describing an illustration must be inserted in its appropriate place in the text and should not be placed on or appended to the drawing.

5. A contribution must terminate with a brief summary of the chief descriptions or observations and any conclusions drawn therefrom. The author is requested to provide the Editor with a type-written abstract of his contribution not exceeding 3% of the text for publication in *Biological Abstracts*.

6. References are to be arranged in alphabetical order of the authors' names at the end of the contribution, the date of the paper being placed in brackets immediately after the author's name. Abbreviations for titles of journals given in the *World List of Scientific Periodicals* should be used. Subject titles should be omitted. In the text a reference to a publication should be cited by giving the author, and, in brackets, the date, thus: "Allis (1934) found, etc."

7. Fifty gratis copies are given to each contributor.

PRINTED IN GREAT BRITAIN BY W. LEWIS, M.A., AT THE UNIVERSITY PRESS, CAMBRIDGE